

Bangor University

DOCTOR OF PHILOSOPHY

Epidemiology of the African armyworm (*Spodoptera exempta*) : intra- and interseasonal variability in outbreak severity in Eastern Africa in relation to weather and moth migration.

Tucker, Michael Richard.

Award date:
1995

Awarding institution:
Bangor University

[Link to publication](#)

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

EPIDEMIOLOGY OF THE AFRICAN ARMYWORM (*SPODOPTERA EXEMPTA*). INTRA- AND INTERSEASONAL VARIABILITY IN OUTBREAK SEVERITY IN EASTERN AFRICA IN RELATION TO WEATHER AND MOTH MIGRATION.

**TW DDEFNYDDIO YN Y
LLYFAGELL YN UNIG
TO BE CONSULTED IN THE
LIBRARY ONLY**

A thesis submitted by
Michael Richard Tucker B.Sc., M.Sc.
for
the degree of Doctor of Philosophy
of the University of Wales
School of Biological Sciences,
University College of North Wales, , Bangor.

April 1995.

Hatari viwavi!
(Beware armyworms!)

This thesis is dedicated to Paula, Matthew and Ruth.

Acknowledgements

This work has been possible only with the help of many organizations and individuals. I would like to thank the directors and the staff of the Kenya National Agricultural Research Centre, Muguga, and Pest Control Services, Tengeru, for making armyworm data freely available, especially: Mr P O Odiyo, Regional Armyworm Forecaster, and staff at the Kenya Armyworm Forecasting Unit; Mr G Mallya and staff at the Tanzania armyworm forecasting unit, Pest Control Services, Arusha; and Mr A Mushi, Assistant Commissioner for Agriculture at the Tanzania Ministry of Agriculture. I am grateful to the Directors and staff of the Kenya Meteorological Department, the Tanzania Meteorological Directorate and the Ethiopian Meteorological Services Agency for making weather data freely available. In addition, I would like to thank the Director-General and staff of the Desert Locust Control Organization for Eastern Africa, (DLCO-EA) especially staff of the DLCO-EA Regional Armyworm Project, to which I was attached for much of this work. Dr D J W Rose, until June 1990, leader of the Regional Armyworm Project, and Mr D E Pedgley, (then at NRI), initiated and supported this work throughout. I gratefully acknowledge the backing I have received from the Natural Resources Institute enabling me to do this thesis, and the assistance and advice of all those at NRI and elsewhere who have commented earlier drafts of this work. I would also like to thank Dr A G Gatehouse, my supervisor at the University College of North Wales Bangor, for his considerable help and advice with this thesis. Finally I would like to thank Dr R Whitehead, Head of the School of Biological Sciences, University of Wales, Bangor for the provision of facilities for part of this study.

Summary

The work described in this thesis aims to improve understanding of the environmental factors affecting the epidemiology of the migratory noctuid moth pest the African armyworm, *Spodoptera exempta* (Walker). The role of weather as a factor causing differences in frequency and location of armyworm outbreaks between seasons is particularly examined. The work is put in context by a review of literature on insect (particularly moth) migration and of the weather and climate of eastern Africa. Armyworm reports and weather records for eastern Africa are analysed for armyworm seasons from 1972-88 and, for a limited dataset, for the beginning of the 1992-93 season. Outbreaks are classified into those derived from low-density populations (primaries) and those from previous outbreaks (secondaries). Moth migrations between outbreaks are estimated from synoptic windfields using trajectory analysis. The association between outbreaks and rainstorms within a season and the relationship between seasonal variations in outbreak frequency and rainfall are investigated. The use of satellite data for identifying rainstorms is described. The results support the hypothesis that outbreaks at the beginning of the season are derived from low-density populations and mostly occur in identifiable 'primary outbreak areas' but that most later outbreaks are secondaries. Severe outbreaks often follow dry periods and persistent rainfall from October to December is associated with low armyworm seasons. Individual outbreaks are associated with the edge of rainstorms supporting the hypothesis that migrating moths are concentrated by rainstorm outflows before outbreak formation. The frequency of particular long-distance moth migrations is discussed in relation to hypotheses about the change in migratory potential of armyworm during the season and the reason for the apparent lack of return migration.

Table of Contents

	Page
List of Figures and Tables	1
Chapter 1.	
Introduction to the epidemiology of migrant insects.	
(a) General background	4
(b) Definition of terms	5
(i) Epidemiology	5
(ii) Outbreaks	6
(iii) Migration	6
(c) The role of migration in the epidemiology of some economically important noctuid moths.	14
(d) African armyworm epidemiology	20
(e) The aims of the present work	28
Chapter 2.	
Weather in eastern Africa and its significance for the epidemiology of African armyworm.	
(a) Climatology	31
(b) Weather systems	37
(c) Weather systems and armyworm moth concentration.	40
(e) Temperature and armyworm development rates	43
Chapter 3.	
Data	
(a) African armyworm data	47
(b) Weather data	49
(c) Location data	52
Chapter 4.	
Classification of outbreaks and seasonal summaries.	
(a) Introduction	53
(b) Methods	55
(i) Outbreaks	55
(ii) Trap catches	56
(iii) Rainstorms	57
(iv) Trajectory analysis	57
(v) Seasonal summaries	60
(vi) Source/destination matrices	61

(c) Results and Discussion	62
(i) Trajectory analysis	62
(ii) Overview	62
(iii) Primary outbreaks	64
(iv) Secondary outbreaks	68
(v) Critical outbreaks	74
(vi) low-density populations	76

Chapter 5.

Frequencies of particular migrations between *Spodoptera exempta* outbreaks and distances covered, based on trajectories.

(a) Introduction	78
(b) Methods	79
(c) Results	81
(i) Migration distances	81
(ii) Migration directions	82
(d) Discussion	84
(i) Migration distances	84
(ii) Migration directions	86

Chapter 6.

Comparison between armyworm seasons.

(a) Introduction	87
(b) Data and Methods	91
(c) Results	93
(d) Discussion	98

Chapter 7.

Forecasting *Spodoptera exempta* outbreaks from rainstorm distribution.

(a) Introduction	100
(b) Rainstorms and outbreaks 1972-88.	103
(i) Data and methods	103
(ii) Results	104
(iii) Discussion	106
(c) Satellite monitoring of rainstorms for armyworm outbreak forecasting.	107
(i) Data	107
(ii) Methods	109

(iii) Results	111
(iv) Discussion	114
Chapter 8.	
General Discussion and Conclusions.	116
Glossary	123
References	126
Appendix	148
Seasonal summaries:	
(i) 1972-73	149
(ii) 1973-74	150
(iii) 1974-75	153
(iv) 1975-76	155
(v) 1976-77	157
(vi) 1977-78	160
(vii) 1978-79	161
(viii) 1979-80	164
(ix) 1980-81	167
(x) 1981-82	170
(xi) 1982-83	173
(xii) 1983-84	174
(xiii) 1984-85	178
(xiv) 1985-86	181
(xv) 1986-87	184
(xvi) 1987-88	187

List of Figures

- Fig 1. Distribution of grassland and wooded grassland in Eastern Africa.
- Fig 2. Location of places mentioned in the text.
- Fig 3. Streamlines of monthly dominant winds over East Africa, November to June.
- Fig 4. Sections through a rainstorm low-level outflow.
- Fig 5. Windflow and insect tracks in the nose of a rainstorm outflow.
- Fig 6. Armyworm head capsule width compared with age after moth arrival leading to oviposition.
- Fig 7. Construction of trajectories of likely moth movements.
- Fig 8. Frequency of early primary outbreaks 1972-87 by degree square and main early season moth migrations.
- Fig 9. Backtracks from early primary outbreaks. 6-23/11/76.
- Fig 10. Backtracks from early primary outbreaks 6-20/11/80.
- Fig 11. Forward tracks from primary outbreaks near Same 16-31/1/82.
- Fig 12. Surface windfield 2/1/77.
- Fig 13. Backtracks from an outbreak at Kahawa 1-15/12/78.
- Fig 14. Backtracks from outbreaks at Moyale and in southern Ethiopia 10-20/5/84.
- Fig 15. Frequency of two degree squares as outbreak sources for further armyworm outbreaks, Oct-Dec.
- Fig 16. Frequency of two degree squares as outbreak sources for further armyworm outbreaks, Jan-June.
- Fig 17. Percentage frequency of moth migration distances between outbreaks.
- Fig 18. Frequency of migrations from source outbreaks in square 0-2S, 36-38E, Oct.-Dec.
- Fig 19. Frequency of migrations from source outbreaks in square 2-4S, 36-38E, Oct-Dec.

- Fig 20. Frequency of migrations from source outbreaks in square 6-8S, 36-38E, Oct-Dec.
- Fig 21. Frequency of migrations from source outbreaks in square 4-6S, 34-36E, Oct-Dec.
- Fig 22. Frequency of migrations from source outbreaks in square 0-2S, 36-38E, Jan-June.
- Fig 23. Frequency of migrations from source outbreaks in square 0-2S, 34-36E, Jan-June.
- Fig 24. Frequency of migrations from source outbreaks in square 2-4S, 36-38E, Jan-June.
- Fig 25. Frequency of migrations from source outbreaks in square 2-4S, 38-40E, Jan-June.
- Fig 26. Time-section of variation in seasonal severity of African armyworm compared with Oct-Dec. rainfall.
- Fig 27. Regression of severity of armyworm season on Oct-Dec. rainfall index.
- Fig 28. Regression of Kenya outbreak severity on Oct-Dec. rains in east-central Kenya.
- Fig 29. Regression of Kenya outbreak severity on previous March-May rains in east-central Kenya.
- Fig 30. Regression of Tanzania outbreak severity on Oct-Dec. rains in Tanzania primary outbreak areas.
- Fig 31. Meteosat 12-hour cold-cloud duration (CCD) for 2-3/11/92, and main armyworm primary outbreak area.
- Figs 32-36. Meteosat 12-hour CCD and location of primary outbreaks for: 10-11/11/92, 14-15/11/92, 16-17/11/92, 18-19/11/92, 27-28/11/92.
- Figs 37-40, : Seasonal summary maps showing primary (bold) 42-52,54: numbers) and secondary outbreaks by month of first occurrence in a degree square, and likely moth migrations between outbreaks (1972-88).
- Fig 41. Backtracks from outbreaks at Kawanda and forward tracks from outbreaks at Singida 18-24/2/76.
- Fig 53. Backtracks from Singida outbreaks 1-31/12/86.
- Fig 55. Backtracks from Kitui outbreaks 18-24/3/88.

List of Tables

- Table 1. Monthly rainfall in eastern Africa.
- Table 2. Monthly frequency of thunderstorm days.
- Table 3. Diurnal variation in rainfall in eastern Africa.
- Table 4. Mean duration of *S. exempta* life-history stages.
- Table 5. Frequency of migrations by $2 \times 2^\circ$ sqs, Oct-Dec.
- Table 6. Frequency of migrations by $2 \times 2^\circ$ sqs, Jan-June.
- Table 7. Long distance armyworm moth migrations and associated winds.
- Table 8. Severity of armyworm seasons in Kenya and Tanzania in relation to location and timing of critical primary outbreaks and rainfall.
- Table 9. Comparison of likelihood of rainstorms in armyworm outbreak moth arrival periods and in the preceding and subsequent 11-day periods.
- Table 10 Location and timing of primary armyworm outbreaks, Nov. 1992.
- Table 11 Number of rainstorms per degree square per week in November 1992 and primary armyworm outbreaks.
- Table 12 Comparison between Meteosat rainstorms data and armyworm outbreak moth arrival periods, Nov.'92.
- Table 13 Monthly rainfall Oct-Dec. 1972.
- Table 14 Rainstorms associated with primary outbreaks, Morogoro region, Jan. 1974.
- Table 15 Monthly rainfall Oct-Dec. 1977.
- Table 16 Monthly rainfall Oct-Dec. 1978.
- Table 17 Monthly rainfall Oct-Dec. 1979.
- Table 18 Rainstorms, outbreaks, E-C Kenya Oct-Nov 1980.
- Table 19 Monthly rainfall Oct-Dec 1982.
- Table 20 Armyworm outbreaks, rainstorms and windshifts, E-C Tanzania, Dec. 1983-Jan. 1984.
- Table 21 Rainstorms, outbreaks, E-C Kenya Oct-Nov 1985.
- Table 22 Rainstorms, outbreaks, E-C Tanzania Oct-Dec 1986.
- Table 23 Rainstorms, outbreaks, E-C Tanzania Oct-Dec 1987.

CHAPTER 1. INTRODUCTION

(a) General Background

The African armyworm *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae) occurs mainly in Africa south of the Sahara, especially in eastern and southern Africa but also in Yemen, parts of the south-east Asia, Australia and Hawaii (Haggis 1984, 1986). Outbreaks of *Spodoptera exempta* caterpillars ('armyworms') cause serious damage to crops and pasture. The adult moths are migratory (Brown and Swaine 1966) and forecasting the occurrence and distribution of outbreaks is a considerable aid to their control.

The present work aims to improve our understanding of the epidemiology of African armyworm outbreaks in relation to environmental factors, especially weather, and with special reference to the role of migration, so as to improve forecasting of outbreaks. The methods used are biogeographical and are based on those that have been developed over many years for the study of migrant insect pests especially locusts and armyworms. The methods are based on the premise that the analysis of changes in distribution of *Spodoptera exempta* populations over time, in relation to environmental factors, can improve understanding not only of African armyworm distribution but also the likely causes of these changes, including the behavioural adaptations of *Spodoptera exempta* to changes in environment.

Firstly the background to the work, in the wider context of the study of migratory insects, is examined starting with a definition of terms to clarify the discussion (a brief Glossary is also included at the end of the thesis).

(b) Definition of Terms

(i) Epidemiology

This term is most commonly used in relation to disease; for example, in Henderson's Dictionary of Biological terms (1989) it is defined as:

'the study of the occurrence of infectious diseases, their origin, cause and pattern of spread through the population'.

In this thesis 'epidemiology' is used with reference to damaging insect pest populations rather than to disease. It is used instead of the more general terms 'population dynamics' or 'population ecology' because the latter terms have, until recently, been generally used for quantitative studies of individual populations, rather than the geographical-scale changes in distribution that are examined in this thesis. Recent work on geographical-scale population analysis has used the term 'geographical population dynamics' (Maurer 1994) and this could be used as a alternative to 'epidemiology' in the present study. However epidemiology also has an implication of sudden upsurge which is appropriate for *Spodoptera exempta*. The definition of epidemiology given above will therefore be modified for present purposes to:

'the study of the occurrence of African armyworm outbreaks, their origin, cause and pattern of spread through the region'.

The emphasis in this study is on the economically important upsurges of armyworm populations that, in some cases, could be called 'epidemics' or 'plagues'. Within such populations, serious damage to crops and pasture is done by individual 'outbreaks'.

(ii) Outbreaks

The term 'outbreaks' refers to high but variable density concentrations of caterpillars that are generally noticed because of the damage they do. Outbreaks often appear suddenly in areas where they were previously absent, due either to an explosive increase in population locally or immigration of parent moths. In some species, such as *Spodoptera exempta*, an additional factor is the density-dependent phase polyphenism of the caterpillars (Faure 1943, Rose 1979). Gregarious (phase *gregaria*) armyworm caterpillars are black, very active and conspicuous and usually occur in high-density outbreaks. Phase *solitaria* armyworm caterpillars are cryptically coloured (green or brown), sluggish and usually occur at very low densities, although occasionally, in thick stands of grass, they may exist at high densities (Langer & Rose 1986).

Intermediate *transiens* phase caterpillars also occur. As outbreaks of gregarious armyworms are both noticeable and cause economic crop damage, it is they rather than the *solitaria* that are reported. The present study is, therefore, primarily a study of armyworm outbreaks.

(iii) Migration

Migration has been defined ecologically as movement out of one habitat into another which, in insects, is usually achieved by flight (Johnson 1969).

Williams (1958) considered that the term 'migration' should be restricted to movement under the insects' control, excluding windborne movement which he considered to be accidental and 'passive'. He gave many examples of such migration, mostly among day-flying butterflies and also hawkmoths (Sphingidae). Perhaps the most well-known such insect migrant is the monarch butterfly (*Danaus plexippus* Linneas) that migrates southwards across north

America in autumn to overwintering sites in Mexico and California, and returns northwards in the spring. Gibo (1986) observed monarch butterflies migrating generally southwestwards in Ontario, Canada in autumn and concluded that they responded to two main selection pressures - selection for minimizing the energetic costs of migration and selection for rapid escape from high latitudes. Butterflies escaped rapidly from high latitudes by flying at high altitudes both in favourable northeasterly winds and in less favourable northwesterly winds which, without compensation would take them away from their destination in Texas. However, they minimized the energetic cost of migration southwards, when winds were southerly or southeasterly, by flying below their 'flight boundary layer' (see p 10) and less frequently.

Johnson took a broader view than Williams and classified migration into three broad classes.

Class I - Insects that emigrate from a breeding site, disperse, oviposit and die.

Class II - Insects that emigrate from a breeding site to a feeding site; the same individuals then return later in the season, after oogenesis, to oviposit in the former breeding site or in others.

Class III - Insects that emigrate from a breeding site to a place where they hibernate or aestivate, the same individual dispersing in the next season, with at least some ovipositing in the territory from which they came.

Johnson considered that most migratory insects were in Class I, which could be subdivided depending on whether the migration was downwind or not, and whether there was any return of a later generation to the source area.

Migration can be defined primarily by its ecological consequences and Taylor and Taylor (1977) have used the term to encompass all ecologically significant displacements. Problems with the definition of 'significant displacement' have, however, led some authors to call all movements 'migration' (Baker 1978). Gatehouse (1987) considered that this was very unsatisfactory and that insect migration should be defined by a behavioural definition such as that used by Kennedy (1961, 1985).

Kennedy's amended (1985) definition was:

'Migratory behaviour is persistent and straightened out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses but promotes their eventual disinhibition and recurrence'.

Johnson (1969) also considered that, in insects, there was a direct physiological relationship between migratory ability and the inhibition of reproductive development (the oogenesis-flight syndrome). In its most extreme form, e.g. in aphids and termites, this results in alate, migratory female insects with undeveloped ovaries and apterous, non-migratory females with fully-developed ovaries. In aphids e.g. *Aphis fabae* (Scop.), however, not all alate females are migratory. The adults of Lepidoptera are nearly always alate but migratory ability in the females is often inversely related to speed of development of the ovaries. Colvin and Gatehouse (1993a) used a tethered-flight technique to examine the flight activity of the noctuid moth *Helicoverpa (Heliothis) armigera* (Hubner) and found that immature moths flew significantly more than did either mature-virgin or

mature-mated moths, which supported the 'ogenesis-flight syndrome' hypothesis.

Southwood (1977) discussed the ecological circumstances in which migration was likely to evolve. The ecological strategy of an animal to maximise the likelihood of survival in spatially and temporally heterogeneous habitats could be summarised in a simple 2x2 matrix labelled 'here' or 'elsewhere', 'now' or 'later'.

Migrations would evolve when 'fitness' (fecundity plus survival) in the new habitat was likely to exceed 'fitness' in the old habitat by an amount greater than the cost of migration. A diapause strategy would evolve where higher 'fitness' was likely to be achieved by reproducing 'here' but 'later'. Some species may use both strategies, while others may continue to develop and reproduce *in situ*. Migration is, therefore, seen as a behaviour evolved in response to habitat changes that tend to result in a decrease in suitability of the source habitat compared with other habitats, in terms of likely 'fitness' of the potential migrant.

These changes in habitat availability and quality may occur regularly, on a seasonal basis, in which case all animals in a particular generation are likely to respond to changes in proximate environmental conditions by migrating, if they are capable of doing so. This migration is 'facultative' if migration does not occur in every generation. 'Obligate' migration, occurring in every generation, is likely to evolve where habitat changes occur at intervals of about one generation, as in areas of very sporadic rainfall. Facultative migration may also occur in response to very irregular changes in environmental conditions. Some species evolve polymorphism, spreading the overall risk by having some individuals which migrate and others that do not. In

some species there is also evidence for an increase in migratory potential in high-density populations e.g. the velvetbean caterpillar, *Anticarsia gemmatalis* Hubner (Hammond and Fescemyer 1987) and the African armyworm, *Spodoptera exempta* (Woodrow et al 1987).

The mechanisms by which insects migrate between habitats have been discussed extensively. Baker (1978), Sotthibandhu & Baker (1987), Baker & Mather (1982) indicated that some moths (*Noctua pronuba* Linneaus and *Agrotis exclamationis*) may use the moon and the earth's magnetic field to orientate themselves when flying. Desert locusts (*Schistocerca gregaria* Forskal) were, perhaps, the first large, strong-flying insects to be shown to move regularly downwind (Rainey 1951, 1963). Swarms consist of streams of locusts that change direction to maintain cohesion, with the net result that the whole swarm is displaced downwind, whether or not windspeeds exceed the air speed of the individual locust (Waloff 1972). In many swarms individual *Schistocerca gregaria* land and feed during the rolling progression of the swarm so, as pointed out by Farrow (1990), although the desert locust swarm is considered to be the most dramatic example of insect migration (defined ecologically), behaviourally it is not really migrating because feeding behaviour has not been suppressed. For most insects, the key factor determining whether they can control their flight direction is whether they are flying above or within their 'flight boundary layer' (Taylor 1958, 1960, 1974). Since wind speeds decrease close to the ground, due to friction with the earth's surface, there is usually a layer within which the wind speed is lower than the insects' flight speed. The depth of this layer varies with insect species, and with wind strength. This is the insects' flight boundary layer (not to be confused with the meteorological planetary boundary layer, which is the layer in which winds are retarded by

friction - Drake & Farrow 1988). Above the flight boundary layer, insects will be carried more or less downwind, no matter in which direction they fly. The realization that insects, such as aphids, may actively initiate such downwind migration in order to cover longer distances, was considered 'a turning point in the study of insect migration' by Kennedy (1961).

The knowledge that many insect species migrate downwind has made it possible to estimate sources and destinations of some insect migrations from synoptic windfield maps, using trajectories of air movement. For such analyses, insect flying times and dates of arrival in or departure from a known location are required. An early such study, by Mikkola and Salmensuu (1965), used geostrophic (300-500 metre) and 850 hPa (1500 metre) winds, derived from weather pressure maps, to estimate sources of an unusual migration of *Spodoptera (Laphygma) exigua* (Hubner) into Finland in 1964. Known migration across Finland was modelled well by trajectories calculated assuming that moths flew all night on geostrophic winds. Backtracks for the earlier part of the migration terminated, after five nights, in a known source area for the moths, east of the Caspian Sea, when moths were assumed to fly by night only at 1500 metres or continuously on geostrophic winds.

More recently atmospheric trajectories have been used to study migrations of brown planthopper (*Nilaparvata lugens* Stal) in eastern Asia (Rosenberg & Magor 1987), of noctuid moths in north America (Wolf et al 1987, Smelser et al 1991) and African armyworm (*Spodoptera exempta*) in eastern Africa (Tucker et al 1982, Tucker 1984). Such studies have provided strong, circumstantial evidence for particular insect migrations.

Further evidence for downwind migration has been provided by studies using radars capable of resolving individual

flying insects. These have conclusively demonstrated that many insects, including species of grasshoppers in West Africa (Riley & Reynolds 1979, Reynolds & Riley 1988), noctuid moths in North America (Wolf et al 1990), East Africa (Riley et al 1983, Rose et al 1985) and Australia (Drake & Farrow 1985), and planthoppers in the Philippines and China (Riley et al 1987, 1991), take-off at dusk and fly actively upwards to heights of several hundred metres where they are carried off downwind. Further evidence for downwind migration has been extensively reviewed by Pedgley (1982).

Taylor et al (1973) investigated the hypothesis that, among Lepidoptera, there is a significant tendency for diurnal migrants (mostly butterflies) to control their direction of flight while nocturnal migrants (mostly moths) are windborne. They analyzed British records of the Silver Y moth, *Autographa(Plusia) gamma* (Linneaus) (Lepidoptera: Plusiidae), a species that flies by night and day, and found a significant tendency for downwind flight to occur at night but not by day. However, their interpretation has been disputed by Baker (1978) who claimed that the differences reflected the higher proportion of moths seen flying over the sea (downwind) at night rather than over land (not downwind). He considered that the results were consistent with moths having preferred compass directions when flying over land. It is, however, possible that the daytime fliers were not migrating (A.G. Gatehouse personal communication).

Another controversy that has not been entirely resolved is whether migration out of a habitat is necessarily followed, at some later time, by a return migration back to the same area. It is now recognized that this is not a simple question, because most species have evolved a range of migratory behaviours, which are often expressed

as polymorphic differences between individuals within a population (e.g. Dingle in: Danthanarayana 1986). This results in a range of migratory abilities so that part of the population would almost certainly be able to find suitable breeding conditions, either close to or far from the original habitat. In species where a substantial part of the population migrates into areas where they cannot survive all year round (e.g. subtropical/tropical moths and butterflies migrating to northern temperate latitudes in summer but being unable to survive the winter) there is likely to be a genetic basis for a return migration (eg Han & Gatehouse 1991). In the northern hemisphere, regular northward migrations of several butterfly species in spring, followed by southward (return) migrations (of a subsequent generation) in autumn have long been demonstrated (Williams 1958). More recently southward (return) migration has been demonstrated by mark-release and recapture and weather analyses in North America for the noctuid moth *Agrotis ipsilon* (Hufnagel) (Showers *et al* 1993). In tropical and subtropical latitudes where rainfall seasonality is more important ecologically than temperature changes, downwind migration towards areas of wind convergence (as has been demonstrated for the desert locust *Schistocerca gregaria* - Rainey 1963) is the most common migration strategy.

The role that migration plays in the life-cycle of insects varies with different insect orders and families, often depending on size and flight ability. The African armyworm (*Spodoptera exempta*) is a noctuid moth. The Noctuidae are a large family (>6000 species) of mostly medium-sized, night-flying moths. They might be expected to develop similar survival strategies in similar environments. A review of research on a variety of economically important noctuid moths should therefore be

relevant to understanding the role migration plays in the epidemiology of African armyworm.

(c) The role of migration in the epidemiology of some economically important noctuid moths

Some species of Noctuidae have long been known to be long-distance migrants (Johnson 1969) but not all noctuids migrate. Among those that do there is considerable variation in migratory potential. Whether a moth species migrates may depend on climate, on the phenology of the larval food plant and on the parts of the plant eaten. Noctuid species feeding on the flowering and fruiting parts of crops (bollworms, budworms, etc) will be described before going on to cutworms and armyworms that feed on leaves and stems, and are therefore likely to have life-history strategies more like that of *Spodoptera exempta*.

The cotton bollworms, *Diparopsis watersi* (Roths) (Sudan bollworm) from Africa north of the equator, and *Diparopsis castanea* Hmps (Red bollworm) from Africa south of the equator, are not known to be migratory but both undergo facultative pupal diapause during the dry season (Tunstall 1958, 1968).

There is evidence for both diapause and migration in the more polyphagous cotton pest *Helicoverpa armigera* (the Old World bollworm or grain podborer). Pupal diapause has long been known to occur in temperate latitudes of Eurasia (Komarova 1959), and moth migration has been demonstrated in the Middle East, and occasionally, on warm southerly winds, to the British Isles by Pedgley (1986, 1985).

In Africa, the evidence suggests that *Helicoverpa armigera* has various strategies. Pupal diapause has been

shown to occur in Botswana, induced by low temperatures and shorter day length in winter (Roome 1979) and (for a very small proportion of pupae) in Tanzania during the dry season (Reed 1965). No diapause was found in Uganda where food plants were available throughout the year (Coaker 1959), or, more recently, in Tanzania, following an increase in maize grown in the cotton off-season (Nyambo 1986). Pupal diapause could be induced in the laboratory in *Helicoverpa armigera* from Sudan, by low temperatures and short day length (Hackett and Gatehouse 1982). Once initiated, diapause continued when temperatures were raised and was ended when temperatures fell, possibly reflecting a mechanism for bridging both the cool dry season and the hot season preceding the summer rains.

In the Sudan Gezira, Haggis (1981,1982) analysed the distribution of *H. armigera* eggs on cotton and found spatial patterns consistent with moths migrating and being concentrated by rainstorm outflows. Topper (1987a, b), however, found evidence for local inter-crop moth flights but not for long-distance migration.

In India, there is circumstantial evidence for some long-distance migration by *Helicoverpa armigera* moths from the east coast to Hyderabad, based on trajectories calculated backwards from periods of increasing light trap catches (Pedgley et al 1987), and from the spread of pesticide resistance (McCaffery et al 1989). Direct observations using mark-recapture (King et al 1990) and aerial netting, infra-red optics and radar (Riley et al 1992) showed emerging moths dispersing at low altitudes (below 10m). The low proportion (7%) of marked moths recaptured in nearby light traps (distances up to 3.5km) suggested, however, that some moths flew at higher altitudes and vacated the area (King et al 1990). This variable behaviour indicated that *Helicoverpa armigera* is a

facultative migrant, first seeking flowering host plants near the emergence site, and only migrating if nearby hosts are unsuitable for oviposition (Riley et al 1992). A genetic component to the regulation of migratory potential has also been demonstrated for *Helicoverpa armigera* (Colvin and Gatehouse 1993).

In north America, both diapause and migration occurs in the corn earworm, *Helicoverpa zea* (Boddie), and the tobacco budworm, *Heliothis virescens* (Forsk.) (Raulston et al 1986). Increases in *Helicoverpa zea* trap catches prior to local emergence from diapause and backtracks, based on surface and 850 hPa winds, gave circumstantial evidence for northward, spring migration from Mexico to Texas and Arkansas (Raulston et al 1986). Direct evidence for northward spring migration by *Heliothis virescens* was obtained by mark-recapture experiments (Raulston et al 1982) and, for both species, by radar studies of moth emergence and flight (Raulston et al 1986, Pair et al 1987, Wolf et al 1990). Pair et al (1987) also found evidence from trap catches for a reverse, southward migration in autumn, from north Texas to south Texas and Mexico.

In Australia the endemic *Helicoverpa punctigera* (Wallengren) is a known long-distance migrant, while *Helicoverpa armigera* is much less mobile there (Farrow and McDonald 1987).

In summary, *Helicoverpa* and *Heliothis* species are both facultative migrants and capable of diapause, the incidence of diapause increasing towards temperate latitudes. The evidence for migration is clearer at the northern edge of the range, when moths may invade areas outside their usual breeding habitat, but it may also occur in the tropics. Diapause and migration are not, therefore, mutually exclusive life history strategies.

Among oligophagous and polyphagous leaf and stem-feeding noctuids, migration is strongly developed in some pest species, but again there is considerable variation. Diapause, however, is not usually present. The new world cotton leafworm, *Alabama argillacea* (Hubner), is known to migrate long distances (Johnson 1969). The Egyptian cotton leafworm, *Spodoptera littoralis* (Boisduval) is less migratory, because although moths are occasionally found at least 50km from known sources, in the deserts of southern Israel and Egypt (Rivnay 1961, Nasr et al 1984), most movement is local, with moths probably flying within their boundary layer (Campion et al 1977, Nasr et al 1984).

The black cutworm (*Agrotis ipsilon* (Huffnagel)) has a near cosmopolitan distribution but is absent from cool temperate latitudes in winter. Its sudden reappearance at latitudes up to 50°N in spring, as documented for 1964 by Odiyo (1975), was assumed to be due to northward migration. This has been confirmed in north America by mark-recapture experiments and atmospheric trajectory analysis (Showers et al 1989, Smelser et al 1991). Northward migration of 100km or more in two to four nights, in June 1984 and May and July 1985, was associated with a low-level jet (windspeeds of 30kph) ahead of depressions over the mid-west USA (Showers et al 1989). As mentioned above, a southward (return) migration by *Agrotis ipsilon* has also been conclusively demonstrated by mark-release-and recapture (Showers et al 1993). This was associated with periods of northerly winds. However the authors assumed, without giving any biological reason, that the moths only flew when there was a northerly airflow. The possibility of migrations in other directions when northerlies were not present was not, therefore considered. *Agrotis ipsilon* is also known to migrate in the Middle East, from Egypt to Israel in

spring, thus avoiding the very hot Egyptian summer (Odiyo 1975).

In north America other noctuid moth pests that have been deduced (from trap catches, weather charts and trajectory analysis) to migrate northwards in spring, on strong, warm southerly winds, include the variegated cutworm, *Peridroma saucia*, the green cloverworm, *Plathypena scabra*, the fall armyworm, *Spodoptera frugiperda* (J E Smith), and the American armyworm, *Pseudaletia unipuncta* (Haworth) (Buntin et al 1990, Wolf et al 1987, Johnson 1987, McNeil 1987). Return migrations have not been conclusively demonstrated although McNeil (1987) and Mitchell et al (1991) give some evidence for *P. unipuncta* and *S. frugiperda* respectively.

In China, the oriental armyworm, *Mythimna separata* (Walker), was shown, by a massive mark-recapture experiment, to migrate at least 1000km north-eastwards in spring (Li et al 1964). A single recapture indicated that south-westward migration in autumn was also possible. More recently migration into north-east China has been observed using entomological radar and confirmed by aerial trapping (Chen et al 1989). These authors considered that a return, southward migration in autumn was unlikely in northern China because northerly winds would be too cold i.e. below 8°C which is the flight threshold for *Mythimna separata*. A return migration would be possible in central China judging by observations of an autumn return migration of brown planthopper (*Nilaparvata lugens*) there using entomological radar and aerial trapping, because the temperature at flying height was 16°C (Riley et al 1991).

Han and Gatehouse (1991) discussed the influence of genetic factors on the length of the pre-calling period in *Mythimna separata* which is the time within which

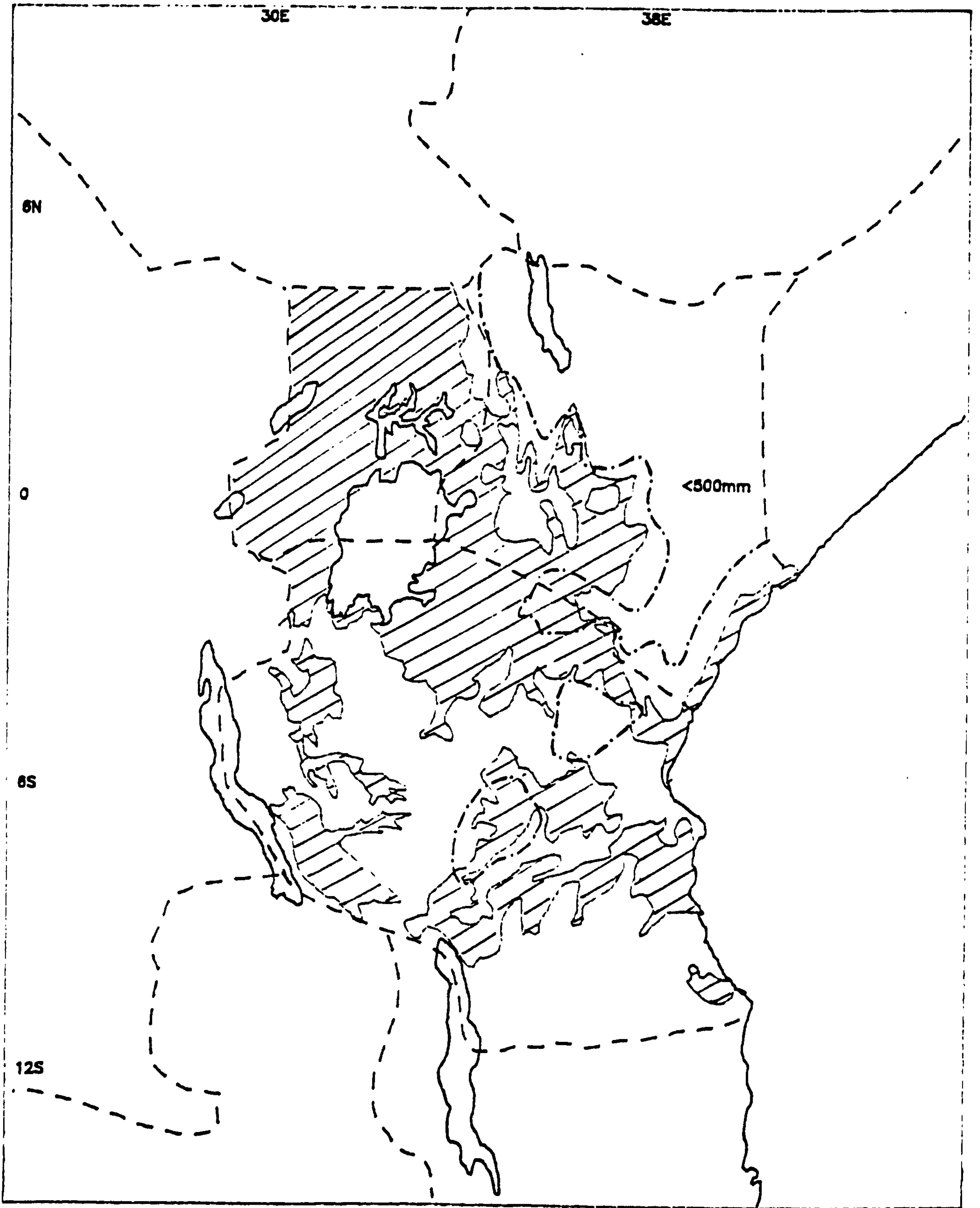
migratory potential may be expressed. They concluded that genetic variation in migration potential would result in stronger migrants penetrating further north, from where their progeny would have a higher probability of migrating southwards than would moths arising from less migratory parents. The direct relationship between the pre-reproductive period and the time available for migration (Johnson's oogenesis-flight syndrome) has been questioned by Sappington and Showers (1992). Their tethered flight work on *Agrotis ipsilon*, indicated that mated females could fly long distances before oviposition. The high migratory ability of both *Mythimna separata* and *Agrotis ipsilon* has not, however, been questioned.

In Australia, the common armyworm, *Mythimna convecta* (Walker), an endemic species feeding on pasture and cereals, is a strong migrant and causes severe outbreaks (Farrow and McDonald 1987, McDonald et al 1990) while the cosmopolitan species *Mythimna separata* and *Spodoptera exempta* are restricted to the east coast and rarely cause outbreaks. Similarly, the endemic black cutworm, *Agrotis infusa* (Boisduval), is a strong migrant while the cosmopolitan *Agrotis ipsilon* is not. Farrow and McDonald (1987) suggested that the cosmopolitan species were relatively recent introductions that have not yet adapted to the natural environment in Australia. *Mythimna convecta* has strong ecological parallels with *Spodoptera exempta* in Africa, in its ability to exploit spatially and temporally variable and unpredictable grassland habitats, and *Spodoptera exempta* (and other cosmopolitan species) may one day adapt to exploit inland grassland habitats in Australia (Gatehouse 1987a). What is known of the epidemiology and life-history strategy of the African armyworm, *Spodoptera exempta*, will now be considered in more detail.

(d) African armyworm epidemiology

African armyworm, *Spodoptera exempta* (Walker), caterpillars feed almost exclusively on cereals and grasses (Gramineae), occasionally on sedges (Cyperaceae) and they have been recorded on coconut palms (Palmae) (Brown 1962, Yarro et al 1981). They are serious pests on maize, sorghum, millet, rice and wheat and, to a lesser extent, on teff, barley and sugar-cane (Odiyo 1979, Scott 1991). They may also cause serious damage to grassland used for animal pasture, reducing livestock productivity both by direct competition for food and by causing a sickness known as 'Kikuyu poisoning' which has killed cattle feeding in areas infested with African armyworm (Brown & Mohamed 1972, Odiyo 1979). The distribution of *Spodoptera exempta* in Africa, as derived from reports of moths and outbreaks (Haggis 1984, 1986) includes the whole of eastern Africa and much of southern Africa from Zambia southwards. In western and central Africa (north of the Equator) the records are patchy but there have been serious outbreaks in several west African countries since 1974. In spite of a few reports of moths, very few outbreaks have been reported from Sudan and there appears to be a gap between *Spodoptera exempta* populations in western and eastern Africa. The natural habitat does not therefore appear to cover all the seasonally dry tropics where grassland and wooded grassland (savanna) are the main vegetation types. In eastern Africa grassland or wooded grassland is the natural vegetation of most of the area between the 500 and 1000mm isohyets and grassland derived from natural forest also occurs widely in wetter areas of Uganda and near the coast of the Indian Ocean (Fig. 1). It has been suggested that the extent and severity of armyworm infestations has increased in recent years, especially in West Africa, due to the increase in area of graminaceous food plants resulting from the

Figure 1. The distribution of grassland and wooded grassland in Eastern Africa (based on Trapnell & Langdale-Brown, 1962). Grassland and wooded grassland are shaded and the 500mm isohyet is shown by a dot-dash line.



clearance of forest and its replacement by crops and grassland (Rainey 1989).

The absence of *Spodoptera exempta* from most of the Sahelo-Sudan grasslands from Sudan to Mauritania is probably due to temperatures that regularly exceed 32°C, which is the temperature at which mortality increases rapidly and fecundity decreases (Hattingh 1941). The main armyworm outbreak areas of eastern and southern Africa are in the highlands where temperatures are considerably cooler. The effect of temperature on *Spodoptera exempta* is discussed later.

The wide availability of food plants in seasonally dry habitats has, almost certainly, contributed to the evolution in *Spodoptera exempta* of a strategy of rapid population increase (with an estimated increase of 100-fold between generations, Rose et al 1978), and dispersal from the emergence site (Rose et al 1985). This is known as an 'r strategy' after the reproductive rate (r) in the logistic equation of population increase and contrasts with the 'K strategy' named after the the carrying-capacity (K) of the habitat (MacArthur & Wilson 1967). Populations of 'K' strategists are relatively stable, being regulated at or near the carrying capacity of the habitat largely by density-dependent factors (Begon & Mortimer 1986). In 'r' strategists density-independent mortality, such as that caused by the effects of weather on the habitat, tends to be more important.

Spodoptera exempta shows a density-dependent polyphenism (Faure 1943) which is also indirectly a response to changes in habitat. The low-density *solitaria* phase and the high-density, *gregaria* phase are the extreme forms but intermediate '*transiens*' forms also occur. The name 'armyworm' comes from the behaviour of gregarious caterpillars which, having defoliated one area, may move

en masse to a new food source. They are also sometimes called 'mystery worms' because outbreaks appear suddenly and erratically, and their distribution in space and time varies from one season to another. Hattingh (1941) noted that widespread outbreaks in South Africa were often related to delays in the onset of the summer rains, and that farmers commonly thought that outbreaks followed droughts. He suggested that, although the timing of the African armyworm season in South Africa was fairly constant (December-March) and depended on temperature, late rains (starting in December-January) resulted in young grass being available to young caterpillars while normal rains (starting in November) resulted in older, tougher and less suitable grass being present in December. Hattingh considered this was evidence that African armyworm outbreaks build up locally rather than through immigration. However Faure (1943) suggested that there were areas such as flood plains and river banks in south-eastern Africa where grasses remained green during the dry season, providing a continuous habitat for *Spodoptera exempta* from which it could invade other areas at the start of the rains.

Following a very severe armyworm season in eastern Africa in 1960-61, a research project was set up under the leadership of E. S. Brown to establish the causes of African armyworm outbreaks and how to forecast them. Brown (1965) suggested that, similar to South Africa, delays in the short rains in eastern Africa (usually October-December) could result in younger grass being available to first armyworm outbreaks than in average years, resulting in higher survival and more severe outbreaks. However, further research indicated that migration was of over-riding importance in the epidemiology of African armyworm (Brown *et al* 1969) and, on the basis of this work, a regional forecasting service

was set up in 1969 (Odiyo 1979, 1984). This was located at the East African Agricultural and Forestry Organisation (EAAFRO), near Nairobi, which became the Kenya Agricultural Research Institute on the break-up of the East African Community. The forecasting service was then transferred to the Desert Locust Control Organisation for Eastern Africa (DLCO-EA) in Nairobi, in 1984. Ethiopia, Kenya and Tanzania also maintain individual country armyworm forecasting units, based in Ministry of Agriculture, Plant Protection or Pest Control departments.

The need for a regional armyworm forecasting service was based on the realisation that armyworm moths migrate long distances, crossing country boundaries and appearing suddenly in previously uninfested areas. This knowledge was originally based on interpretation of trap catches (Brown and Swaine 1966) and mapping of outbreak distributions (Brown et al 1969). In east Africa, armyworm outbreaks are first reported in about November and may be present until July. From March to July of many years, outbreaks are reported progressively further north from Tanzania and Kenya to Ethiopia and Yemen (Haggis 1984, 1986). Brown et al (1969) showed that this could be attributed to large-scale moth migration following the seasonal wind change from north-easterly or easterly to south-easterly or southerly. The last outbreaks in Ethiopia and Yemen occur in August or September. Rainey and Betts (1979) considered that there were then one or more unreported generations of outbreaks linking Ethiopian outbreaks with the first outbreaks in Kenya or Tanzania. However, no convincing evidence was presented for a return migration, as required by this hypothesis. Although Brown et al (1969) found an association between first outbreaks of the season in Kenya and Tanzania (from October to December) and windshifts from southeasterly to northeasterly (for 1963-

67), Tucker (1984a) found from backtracks (for 1966-80) that likely sources of moths leading to first outbreaks were usually in the eastern parts of these countries, not further north, because the easterly components of the winds predominated.

Direct evidence for armyworm moth migration has been obtained from radar observations and a mark-capture experiment (Riley et al 1983, Rose et al 1985). It was found that moths flew upwards from outbreak emergence sites and migrated downwind at heights of several hundred metres, for distances of up to at least 90km, and probably 147km, in one night. The total duration of moth flight depends on both the length of the pre-reproductive period (PRP) (Page 1988, Wilson & Gatehouse 1992) and the flight capacity of the individual moths (Parker and Gatehouse 1985a,b, Woodrow et al 1987). In laboratory experiments on moths emerging from pupae taken from different outbreaks, PRPs were usually one to two nights for males and one to five nights for females but delayed development sometimes occurred resulting in PRPs up to seven nights for males and 13 nights for females (Wilson & Gatehouse 1993). Migration distances can, therefore, vary considerably between moths and this, together with the tendency of moths to disperse during downwind migration (Riley et al 1983) means that if subsequent outbreaks are to form there must be some mechanism for reconcentrating the moths before they lay eggs. Haggis (1971) found an association between high hourly catches of armyworm moths and sharp changes in wind direction (windshifts). Douthwaite (1978), however, using much the same data, concluded that the association was due to higher catches occurring in periods of light winds than strong winds, irrespective of whether the light winds were associated with windshifts or not. Douthwaite did find a tendency for larger moth catches to occur in wet hours than in dry hours. Direct evidence, from radar

observations, has shown that low-level outflow winds from rainstorms can concentrate flying moths (Pedgley et al 1982, Riley et al 1983) and a significant association between outbreaks and rainstorms at the time of moth concentration prior to oviposition has been found (Tucker and Pedgley 1983).

Rose (1979), using data from Zimbabwe including a study of an outbreak in relation to synoptic weather patterns (Rose & Law 1976), proposed that the first armyworm outbreaks of a season arise when moths emerging from low-density, *solitaria* populations are concentrated by convergent wind patterns. Some evidence for the persistence of low-density, *solitaria* armyworm populations between outbreak seasons comes from the occasional capture of small numbers of moths in traps during the 'off-season' (July to October) in Kenya and Tanzania (Odiyo 1981). There is strong evidence for the persistence of low-density armyworm populations in Malawi, where moths are caught in pheromone traps throughout the year, although outbreaks generally occur only from November to April (Nyirenda 1985).

Robinson (1991) developed a model for predicting monthly changes in African armyworm distribution in eastern Africa from an index of vegetation greenness (the normalised difference vegetation index or NDVI) , derived from NOAA satellite data and from lower and upper mean monthly temperature thresholds of 17°C and 27°C respectively.

NDVI is calculated from Channel 1 (red) and Channel 2 (infra-red) spectral wavebands by the formula:

$$\text{NDVI} = (\text{Channel 2} - \text{Channel 1}) / (\text{Channel 2} + \text{Channel 1})$$

Results from this model indicated that coastal areas of Kenya and Tanzania, Uganda, western Tanzania and much of southern Tanzania may be suitable for armyworm development from May to October. This period is the dry season in southern Tanzania and the apparent greenness is almost certainly due to the predominance of perennial woodland vegetation rather than green grass. This suggestion is supported by a study comparing the relation between rainfall and NDVI in east Africa (Davenport & Nicholson 1993) which found that NDVI was sensitive to vegetation changes following rainfall in dry bushland but not in generally wetter areas, such as southern Tanzania. It is unlikely, therefore, that armyworm can persist throughout the year in southern Tanzania. It is not known whether low-density armyworms do survive in Uganda and western Tanzania but small numbers of moths have been caught on the coasts of Kenya and Tanzania, indicating that populations do persist there (see above). Other aspects of this model are discussed later.

Laboratory experiments on the flight performance of individual armyworm moths showed there was a genetic component in the determination of flight capacity (Parker & Gatehouse 1985b). When this was taken into account by genetically matching samples, it was found that female armyworm moths derived from high-density, *gregaria* phase caterpillars flew significantly longer than those from low-density, *solitaria* phase caterpillars (Woodrow et al 1987). Gatehouse (1987) suggested that higher migratory potential in moths derived from high-density, outbreak populations evolved to enable armyworm moths to disperse rapidly from outbreaks and so avoid the adverse effects of high density, such as limiting food resources and increases in natural enemies and disease in subsequent generations. Parker & Gatehouse (1985b) further argued that migratory potential was likely to be highest early in the rainy season when suitable habitats were patchy

and widely scattered, and lower late in the season when green grass would be widespread. This model was tested by Wilson & Gatehouse 1993, who quantified the variation in pre-reproductive period (PRP) of moths from fourteen different outbreak sources in eastern Africa. They found extensive intra- and inter-population variation in PRP. PRPs were longer for females (median 3 nights, range 1 - 13 nights) than for males (median 1.5 nights, range 1 - 7 nights). Mean PRP was inversely correlated with rainfall at the outbreak site in the month moths initiating the outbreak arrived. Longest PRPs (means of 2.5 - 5.5 nights) occurred in moths originating from early season outbreaks in regions of low, variable rainfall and shortest PRPs (means of 1 - 3 nights) in moths from areas of high, consistent rainfall. Mean PRP of moths tended to decline during the long rainy season in Kenya and Tanzania. Thus, at the end of the rains the armyworm population is likely to be less mobile but widely dispersed, increasing the likelihood of some armyworm surviving the dry season in suitable habitats and possibly explaining the apparent lack of return migration in outbreak populations (Gatehouse 1987).

Outbreaks suspected of being caused by moths coming from low-density populations, especially those at the beginning of the season, have been called 'primary' (Rose *et al* 1987, Pedgley *et al* 1989) to distinguish them from 'secondary' outbreaks derived from moths coming from previous outbreaks. Although it is usually assumed, based on previous work, that moths leading to both primary and secondary outbreaks have migrated to the outbreak site, there is nothing in the definitions that presuppose migration, and in theory, both primary and secondary outbreaks could result from a local, previous generation. The formation of primary outbreaks from previous low-density populations is thought to be of particular importance in armyworm epidemiology and the

development of the armyworm season in eastern Africa. Furthermore, a strategy has been developed, in eastern Africa, to control primary outbreaks, especially those (termed 'critical') which, if left uncontrolled, would lead to many secondary outbreaks in cereal growing areas, following downwind migration (Rose et al 1987). Further understanding of armyworm epidemiology would help improve both forecasting and control strategy.

(e) The aims of the present work

The work described in this thesis aims to improve understanding of the environmental factors affecting *Spodoptera exempta* epidemiology, especially the differences in frequency and location of armyworm outbreaks between seasons.

The assumptions are:

(i) African armyworm outbreaks can be classified into two distinct categories - 'primary' and 'secondary' and that these can be identified using backtrack analyses to estimate sources of parent moths leading to the particular outbreaks;

(ii) outbreaks can further be classified into 'critical' or 'non-critical' depending on whether or not many subsequent outbreaks are likely to have been derived from them;

(iii) synoptic weather data can be used to estimate likely moth migrations;

(iv) significant spatial and temporal associations between armyworm outbreaks and weather events are likely to have a causal relationship;

(v) available data on African armyworm occurrence, while not necessarily complete, reasonably represent the actual distribution of outbreaks.

A number of hypotheses can be postulated arising from previous work and the above assumptions. These are:

(i) the first outbreaks of the season in Kenya and Tanzania are primary ie. derived from low-density populations (H_1).

(ii) primary outbreaks occur in identifiable areas that can be called 'primary outbreak areas' (H_2).

(iii) most outbreaks after the beginning of the armyworm season are secondary, indicating that during the season continuity of outbreak populations is more important than gregarisation from low-density populations (H_3).

(iv) alternatively that most outbreaks throughout the season are primary ie are derived from low density populations, and that there is little continuity between outbreaks (H_4).

(v) outbreak formation is often associated with rainstorms (H_5).

(vi) seasonal variations in outbreak frequency are largely caused by seasonal variations in environmental factors especially weather and climate (H_6).

In order to test these hypotheses, records for 16 seasons 1972-73 to 1987-88 were used to:

(i) identify primary and secondary outbreaks, their most frequent areas of occurrence and their relation to weather, especially rainfall and winds;

- (ii) examine likely moth migrations between outbreaks and the role of migration in African armyworm epidemiology;
- (iii) identify critical outbreaks;
- (iv) discuss the role of low-density armyworm populations;
- (v) summarize the development of each armyworm season to enable them to be compared with other seasons;
- (v) examine inter-seasonal differences in overall severity in relation to the timing and location of primary outbreaks and early season rainfall;
- (vi) describe techniques that can be used to improve armyworm forecasting and control strategies, especially those involving environmental monitoring from satellites.

CHAPTER 2. WEATHER IN EASTERN AFRICA AND ITS SIGNIFICANCE FOR THE EPIDEMIOLOGY OF AFRICAN ARMYWORM

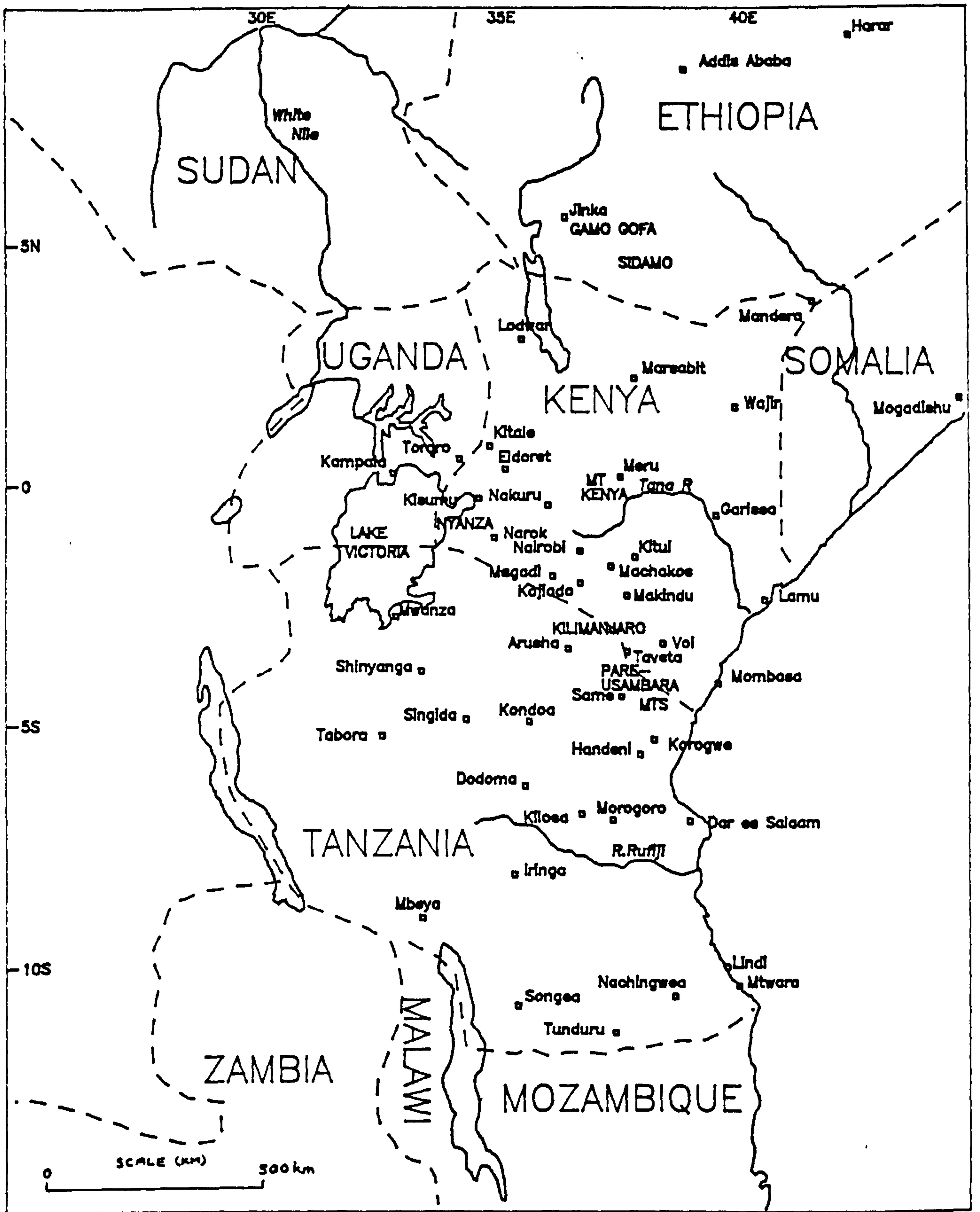
Weather has an important role in *Spodoptera exempta* moth migration, in outbreak formation and in the survival of both larvae and adults. A basic understanding of the climate and weather in eastern Africa is essential for forecasting armyworm outbreaks there, so a summary of the main features is given here. Details of particular events affecting armyworm are given in the seasonal summaries in Appendix 1.

(a) Climatology

The climate of eastern Africa is notable for a widespread rainfall deficiency, compared with other equatorial locations, that has been called 'the most impressive climatic anomaly in all of Africa' (Trewartha 1981). Table 1 shows mean monthly rainfall totals for selected stations in Kenya, Tanzania and Uganda (Kenya Meteorological Department 1984, East African Meteorological Department 1975). The location of these stations is shown in Figure 2. Because much of eastern Africa consists of plateaux and highlands at elevations exceeding 1000m, air temperatures, which decrease with increasing height, are strongly affected. Air temperatures affect both the distribution and the development rate of *Spodoptera exempta* and will be considered separately later.

Humid climates, with mean annual rainfall totals exceeding 1000 mm, occur only in the western Ethiopian highlands, Uganda, western Kenya and Tanzania near Lake Victoria, the Indian Ocean coast south of 3°S, and parts of the highlands of central Kenya, and north-eastern and southern Tanzania (Tomsett 1969 and Table 1). The remainder of eastern Africa has been classified as semi-

Figure 2. Location of places mentioned in the text. Towns are in lower case letters and countries, regions and mountains are in capitals.



arid or arid (Pant & Rwandsya 1971). Arid climates, with mean annual rainfall totals of less than 600mm, occur in eastern Ethiopia, Somalia, northern and eastern Kenya, and parts of northern and central Tanzania (e.g. Lodwar, Garissa, Voi, Same and Dodoma in Table 1).

This widespread aridity can largely be explained with reference to the dominant windfields. Figure 3 shows the dominant low-level, daytime winds in east Africa for November to June, the main armyworm season months (Tucker *et al* 1982). Dominant winds are generally easterly but vary from mostly east to north-easterly from December to February, to southeasterly to southerly from April to October, with the change-over occurring in March and November. The convergence between these winds (the Intertropical Convergence Zone) is not a well-defined feature in east Africa (unlike West Africa and Sudan). Its presence across east Africa corresponds approximately to the period of easterly winds in March and November, but windfields are strongly modified by the highlands and there are occasional periods of westerly winds. Nevertheless, there is a northward and southward shift of the Equatorial Pressure Trough (associated with mean wind convergence and rainfall) following the relative movement of the overhead sun (Hills 1979 and Figure 3).

In southern and central Tanzania (south of about 6°S), the period of north-east to east winds (November to March) is the rainy season but in Kenya these winds have a largely overland trajectory, from Somalia and Arabia, and are dry (Trewartha 1981). In northern Tanzania and south-western Kenya, south-easterly winds persist during November to March, caused by deflection around the highlands of northern Tanzania and southern Kenya, and resulting in widespread divergent (subsiding) airflow and dry weather (Figure 3).

MISSING PAGES
REMOVED ON
INSTRUCTION
FROM THE
UNIVERSITY

From May to September the south-easterly to southerly winds are divergent at low-levels, with winds near the coast veering to south-westerly as they join the Indian south-west monsoon circulation and winds inland deflected to easterly by the Ethiopian highlands. The parallelism of these winds to the Indian Ocean coast, and the upwelling of cold water in the cool Somali ocean current, add to the divergent effects to increase the aridity of Somalia and eastern Kenya (Flohn 1965, Trewartha 1981). Another factor is the position of these lowlands in the lee of the east African highlands, with respect to incursions of moist westerly winds (Nakamuru 1967). Above the surface, a low-level jet of strong southerly winds occurs over eastern Kenya, with windspeeds of 12-20ms⁻¹ at 1,000m as recorded at Garissa and Voi (Findlater 1966, 1967, 1969). This jet forms a western boundary current of the Indian Ocean southwesterly monsoon (Anderson 1976) and varies in strength, partly depending on whether the air stream originates to the west or east of Madagascar (van de Boogaard & Rao 1984).

A strong south-easterly low-level jet is also present, throughout the year, in the low-lying Turkana region of northern Kenya (Kinuthia & Asnani 1982). Mean monthly morning wind speeds exceeding 25ms⁻¹ are caused by the channelling of easterly winds between the Ethiopian and Kenyan highlands.

In contrast to eastern Kenya and Somalia, the Ethiopian highlands have a rainy season from May to September. This is caused by convergence associated with the Intertropical Convergence Zone and the development of an area of heat-induced low pressure over the highlands. This is also associated with anabatic (upslope) winds, frequent moist southwesterly winds from central Africa and convective rainfall (Flohn 1965, Trewartha 1981).

In Kenya and northern Tanzania there are two rainy seasons, the 'long rains, from March to May and the 'short rains' from November to December. These follow the northward and southward shift of the overhead sun respectively, and correspond to the maximum occurrence of onshore easterly winds. Local variations due to topography and proximity to moisture sources obscure this zonal pattern on isohyet maps but it can be seen when monthly rainfall totals are expressed as a percentage of the annual mean for that station (Neiuwolt 1974). Table 1 uses this method, with stations approximately from north to south. It shows changes in the rainy seasons with latitude but also considerable regional variations. In Kenya east of the Rift Valley, but excluding the coast, about 75% of the annual rainfall falls in the long and short rains, but this proportion decreases westwards to less than 50% at Nakuru and Eldoret where the long rains continue into June, July and August. These 'dry' season rains are associated with the frequent occurrence of large-scale westerlies at about 2.5 - 5km altitude, interacting with the Kenya highlands, in these months (Nakamura 1968, Davies et al 1985). In Kenya, these upper-level westerlies are infrequent at other times of year, but in southern Tanzania they occur during the rainy season from November to April (Nakamura 1968). These winds are above known armyworm flying heights (even over the highlands) so large-scale eastward moth movements are only likely when westerlies descent towards the surface in the armyworm season (October to June). Such surface westerly winds do occur occasionally, especially west of 36°E, and most frequently in the rainy seasons. The convergence zone between these, usually light, westerlies and the dominant easterlies is known as the Zaire air boundary (Congo air boundary or African Rift convergence). Surface westerlies are often associated with rainstorms, although many reports of such associations refer to mesoscale, downdraught outflow

winds from the storms, rather than large-scale westerlies.

In Uganda, winds are frequently light and variable and the presence of moist air from Lake Victoria and from Zaire can result in rain in any month. There are, however, rainfall peaks in April to May and November at most stations (Table 1). On the Indian Ocean coasts of Kenya and Tanzania the dry seasons are less severe than inland and, on the Kenya coast, the long rains frequently persist until July.

Seasonal differences in climate have a considerable effect on the epidemiology of African armyworm. Tucker (1984b) and Harvey (1992) found inverse relationships between October to December rainfall and the severity of the armyworm season. Tucker used area mean rainfall for different primary outbreak areas and contingency tables, to compare the occurrence of above or below mean seasonal rainfall with high or low numbers of armyworm outbreaks in Kenya and Tanzania. He found a significant inverse relationship for rainfall in Kisumu, Morogoro and Mtwara areas and for all areas combined. Harvey used rainfall (and river flow) data for east-central Tanzania and found an inverse correlation between November rainfall (and river flow) and annual moth catches at traps in Tanzania.

Moerth (1970), using river basin area rainfall for 1938-67, found that large anomalies in rainfall usually occur in the same direction over the whole of eastern Africa and this was largely confirmed by Nicholson & Entekhabi (1986) who looked at rainfall anomalies over the whole of Africa. Rodhe & Virji (1976) analyzed annual rainfall for 35 stations in east Africa for more than 44 years, for trends and periodicities. They found no long-term trend but spectral analysis gives peaks at 2-2.5, 3.5 and 5-5.5 years, indicating cycles in total rainfall. These

cycles were confirmed by Nicholson & Entekhabi (1986) who found a significant relationship between variations in rainfall and a large-scale, Southern-Hemisphere, meteorological feature known as the Southern Oscillation. This is measured as an index of sea-level pressure difference between Tahiti and Darwin (Australia) and has been found to have global effects on climate (Ropelewski & Halpert 1987). Nicholson & Entekhabi found an inverse relationship between the Southern Oscillation Index and rainfall in equatorial Africa and a positive relation for other areas of Africa. The Southern Oscillation Index (SOI) is inversely correlated with the occurrence of El Nino, when sea-surface temperatures off the Peruvian coast increase, leading to heavy rainfall in this normally dry area. Ropelewski & Halpert (1987) confirmed a positive relationship between October to April rainfall in the area surrounding Lake Victoria and the occurrence of El Nino (low SOI), and a negative relationship for most of southern Africa. Farmer (1988) found a negative correlation between the SOI and September to December rainfall on the Kenyan coast ($R = 0.51$) suggesting the possibility of using the June to August SOI to predict these rains. Hutchinson (1992) has found a similar inverse correlation between SOI and rainfall in southern and central Somalia. Thus, for most of eastern Africa, there is some possibility of predicting 'short rains' rainfall from the preceding SOI, and this may be significant for seasonal armyworm forecasting.

Climate is a dominant factor controlling the evolution of natural vegetation and of animal species. The African armyworm, *Spodoptera exempta*, can, therefore, be expected to have adapted to the seasonal climate changes within eastern Africa. Individual populations are directly affected by weather events occurring at particular stages of their development. Changes in climate may result in more or less frequent rainstorms, which in turn may

determine the frequency of armyworm outbreaks and the survival of the caterpillars. The occurrence of individual weather events is now considered.

(b) Weather systems

In the tropics, the main synoptic-scale weather systems (defined as systems with horizontal scales of 500 to 2000 km and time-scales of the order of 100 h - Barrett 1974) are tropical cyclones, tropical depressions (including monsoon depressions) and easterly waves (Riehl 1979).

Tropical cyclones forming in the southern Indian Ocean (between 5 and 14°S) in the period November to May, sometimes penetrate the Mozambique Channel and affect the weather of south-eastern Tanzania, and very occasionally an Arabian Sea tropical cyclone affects the eastern tip of Somalia, in the northern hemisphere spring and autumn (Gray 1979). Most of eastern Africa is, however, unaffected by tropical cyclones or tropical depressions.

Johnson (1962) studied day-to-day variations in rainfall distribution and found no evidence for mobile rainbelts crossing east Africa. He concluded that equatorial or easterly waves, such as are found in west Africa and the Caribbean, contribute little to east African weather. Johnson's analysis was based on percentages of stations, in areas of about 1° square, having rainfall on a particular day. Isohyets (lines of equal rainfall amount) were not used because of the patchy nature of tropical rainfall and the large diurnal variations. These analyses showed that, apart possibly from Uganda, precipitation was not randomly distributed in space and time, but occurred in evolving quasi-stationary synoptic-scale systems. These developed in periods of one to two days and persisted for several days.

Johnson & Moerth (1963) went on to explain the development and decay of these systems in terms of divergence or convergence in upper level (700hPa or approximately 3000m altitude) pressure patterns. The most frequent patterns were the Equatorial duct (with easterly winds between high pressure on either side of the equator) and Equatorial drift (with low pressure on one side of the equator and high pressure on the other causing airflow across the equator). These patterns are similar to dominant wind patterns near the equinox and in the northern hemisphere summer respectively, but Johnson & Moerth (1963) showed that patterns changed over periods of a few days, as well as on a seasonal basis. Advection of moist air was found to be particularly associated with patterns giving rise to upper-level westerly winds (as also found by Nakamura 1968).

Synoptic systems provide the overall dynamic, meteorological environment in which rainstorm development is either encouraged (low-level convergence and moist air) or inhibited (low-level divergence and dry air). Nieuwolt (1974a) investigated the distribution of heavy rainstorms (>25mm rain in 24 hours), that were likely to cause erosion, in Tanzania. He concluded that development of these rainstorms was largely controlled by local topography, and they were most frequent in the southern highlands, near Kilimanjaro and near the moisture sources of the Indian Ocean, and the Lakes Victoria, Nyasa and Tanganyika. Kuhnelt (1991), on the other hand, concluded, from daily visible satellite imagery, that cloudiness patterns over east Africa largely reflected a mixture of influences from neighbouring areas (east, west, north and south of east Africa). Sumner (1981, 1983, 1984) found that rainstorms at Dar es Salaam were predominantly linear or elliptical in shape and orientated parallel to the coast, often along land or sea-breeze fronts. Inland in Tanzania,

south of Lake Victoria, Sharon (1974) examined the distance-correlation relation of daily rainfall. He found that correlation between stations decreased up to about 20km but increased again to a second maximum at 40-60km, irrespective of direction. This indicated that rainfall was organized in convective cells centred 40-60km apart.

Barring (1987) examined spatial patterns of daily rainfall in central Kenya, using principal components analysis, common factor analysis and spatial correlation. He found that the area could be divided into an area east of a line from Mt Kenya to the southern Aberdare highlands with two distinct rainy seasons, and an area to the west with more complex, less distinct rains. In December to March (and to a lesser extent April to May), rainstorm distribution was near-random but, in June to September (and to a lesser extent in October to November), rainfall was organized on a NE to SW alignment. The latter was due orographic influences (of Mt Kenya and the Aberdare highlands) affecting south-easterly winds. The distribution of rainstorms, therefore, varies with location and season. Low-level outflow of air from intense rainstorms, which are usually thundery, has been shown to concentrate flying moths prior to armyworm outbreak formation (Pedgley et al 1982). The distribution and frequency of thunderstorm days (Table 2, from Chaggar 1977) is therefore useful for assessing the likelihood of convergent winds suitable for armyworm moth concentration.

The number of thunderstorm days is remarkably high, throughout the year, near Lake Victoria, at Kisumu, Kampala and Tororo. This results from the interaction of the lake breeze and the large-scale windflow, which causes late afternoon to evening thunderstorms at Kampala but mostly early morning thunderstorms at Entebbe, near

Kampala (Lumb 1970). On the southern shore of Lake Victoria, at Mwanza, thunderstorms are frequent from October to May, but less so during the dry season months of June to September. Thunderstorms are frequent during the rainy season months in most of Tanzania, with a mean of about ten thunderstorms in each month from December to March, except for Mbeya (in the south-west) where there are more, and north-east Tanzania (Arusha, Same and Tanga) where there are fewer. In Kenya, thunderstorms are most frequent in the west, at Eldoret and Nakuru during the period April to September, and at Narok in March-April. Elsewhere thunderstorms are much less frequent with an average of 4.5 thunderstorm days per month in the long rains and 2.5 in the short rains, with almost none from June to October.

As armyworm moths fly at night, the diurnal distribution of rainfall should indicate the likelihood of moths being concentrated by rainstorm low-level outflows. Table 3 (Tomsett 1975) shows that, away from the Indian Ocean coast and Lake Victoria, most rain falls in the afternoon or night (from 1200 to 2400 or 0300 hours at most stations, but to 0600 at Nairobi and Makindu). The frequencies indicate that, at most places, when rainfall occurs on a particular day, there is a greater than 50% chance that it fell during the hours 1800 to 0600, when armyworm moths may be flying.

(c) Weather systems and armyworm moth concentration

The mechanisms by which flying armyworm moths may be concentrated by winds have been discussed by Pedgley (1990) and on P24. Synoptic-scale wind convergence, measured as rate of change in volume per second, is typically about 10^{-5}s^{-1} , which would result in a tenfold increase in volume density only after several days. However, convergence in meso-scale systems, such as

rainstorm outflows, is much stronger (10^{-3}s^{-1}), resulting in a tenfold increase in volume density in about an hour. Intense convective rainstorms typically last for one or two hours, so flying moths caught up in them might be expected to be concentrated by 10 or 20 fold. If these moths landed, before being re-dispersed, the increase in area (as distinct from volume) density would be 100 to 400 fold. This might well be sufficient to cause armyworm outbreaks, following oviposition.

Figure 4 gives a diagrammatical vertical section and plan view of a typical convective rainstorm. Heavy rain falling from the cloud base cools the underlying air, so that a downdraught of cool, dense air is formed. On approaching the ground surface this downdraught spreads out, undercutting the warmer, less dense surrounding air, which is feeding into the rainstorm. An abrupt change in wind direction and increase in wind speed accompanies the outward spreading downdraught. At this squall-line, low level winds are convergent and any insects flying within them are concentrated, as has been seen by radar (Figure 5). A tendency for insects then to be carried upwards and into air returning towards the rainstorm appears to be resisted by the insects (Achte-meier 1991). As they enter cooler, high-level air they usually fly downwards and may land, with the effect that they are concentrated at the gust front.

Rainstorm low-level outflows are a particular type of density current. Other atmospheric density currents include sea and lake breezes, which are caused by the differential heating of land and water, with cool, dense air moving inland at low-levels in the afternoon, undercutting air warmed by daytime heating. The warm air rises and moves seaward (or lakeward) at several kilometres altitude to complete the circulation.

MISSING PAGES
REMOVED ON
INSTRUCTION
FROM THE
UNIVERSITY

rainstorm outflows, is much stronger (10^{-3}s^{-1}), resulting in a tenfold increase in volume density in about an hour. Intense convective rainstorms typically last for one or two hours, so flying moths caught up in them might be expected to be concentrated by 10 or 20 fold. If these moths landed, before being re-dispersed, the increase in area (as distinct from volume) density would be 100 to 400 fold. This might well be sufficient to cause armyworm outbreaks, following oviposition.

Figure 4 gives a diagrammatical vertical section and plan view of a typical convective rainstorm. Heavy rain falling from the cloud base cools the underlying air, so that a downdraught of cool, dense air is formed. On approaching the ground surface this downdraught spreads out, undercutting the warmer, less dense surrounding air, which is feeding into the rainstorm. An abrupt change in wind direction and increase in wind speed accompanies the outward spreading downdraught. At this squall-line, low level winds are convergent and any insects flying within them are concentrated, as has been seen by radar (Figure 5). A tendency for insects then to be carried upwards and into air returning towards the rainstorm appears to be resisted by the insects (Achteemeier 1991). As they enter cooler, high-level air they usually fly downwards and may land, with the effect that they are concentrated at the gust front.

Rainstorm low-level outflows are a particular type of density current. Other atmospheric density currents include sea and lake breezes, which are caused by the differential heating of land and water, with cool, dense air moving inland at low-levels in the afternoon, undercutting air warmed by daytime heating. The warm air rises and moves seaward (or lakeward) at several kilometres altitude to complete the circulation.

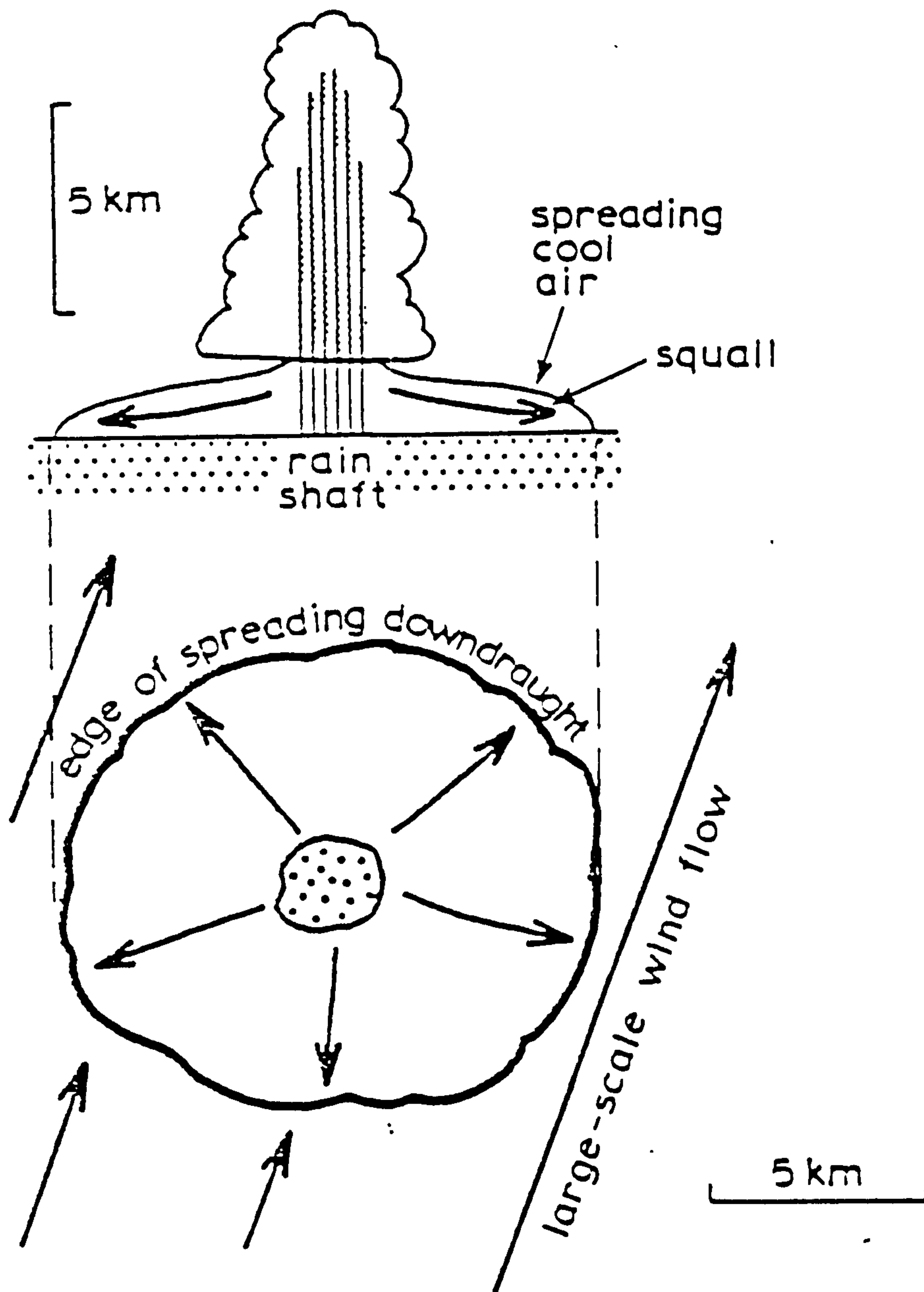


Figure 4. Diagrammatical vertical and horizontal sections through a rainstorm low-level outflow (from Pedgley 1982).

Flying insects have been shown, by radar observations in southern Australia, to be concentrated by sea-breezes (Drake 1982). Similarly, lake breezes such as those caused by Lake Victoria, often have a well developed, meso-scale front where insects are likely to be concentrated. In this particular case, the lake-breeze front is also often associated with thunderstorms (Lumb 1970), increasing the likelihood of moth concentration in the vicinity.

Other atmospheric features can also concentrate flying insects. Topography can induce a variety of blocking, channelling and buoyancy effects in the windfield. Downwind of hills, reversals of airflow, in the form of horizontal or vertical rotors, are frequently formed, especially at night when the air is stably stratified (Pedgley 1990). Armyworm moths have been shown, by radar observations, to be concentrated in rotors, formed downwind of the steep eastern escarpment of the Kenyan Rift Valley (Pedgley *et al* 1982). The rotor consisted of an overturning circulation but concentration occurred where the low-level returning westerly winds met the undeflected easterlies, resulting in a cross-section similar to that for a density current (Figure 5).

Drake & Farrow (1985), using an entomological radar, observed horizontal concentrations of migrating moths in a stably stratified, nocturnal atmosphere in southern Australia, and Drake (1984, 1985) similarly observed linear concentrations of insects associated with solitary wave disturbances of the nocturnal boundary layer. In these instances, large increases in insect density at ground level were only likely when overturning circulations formed, disrupting the vertical distribution of insects.

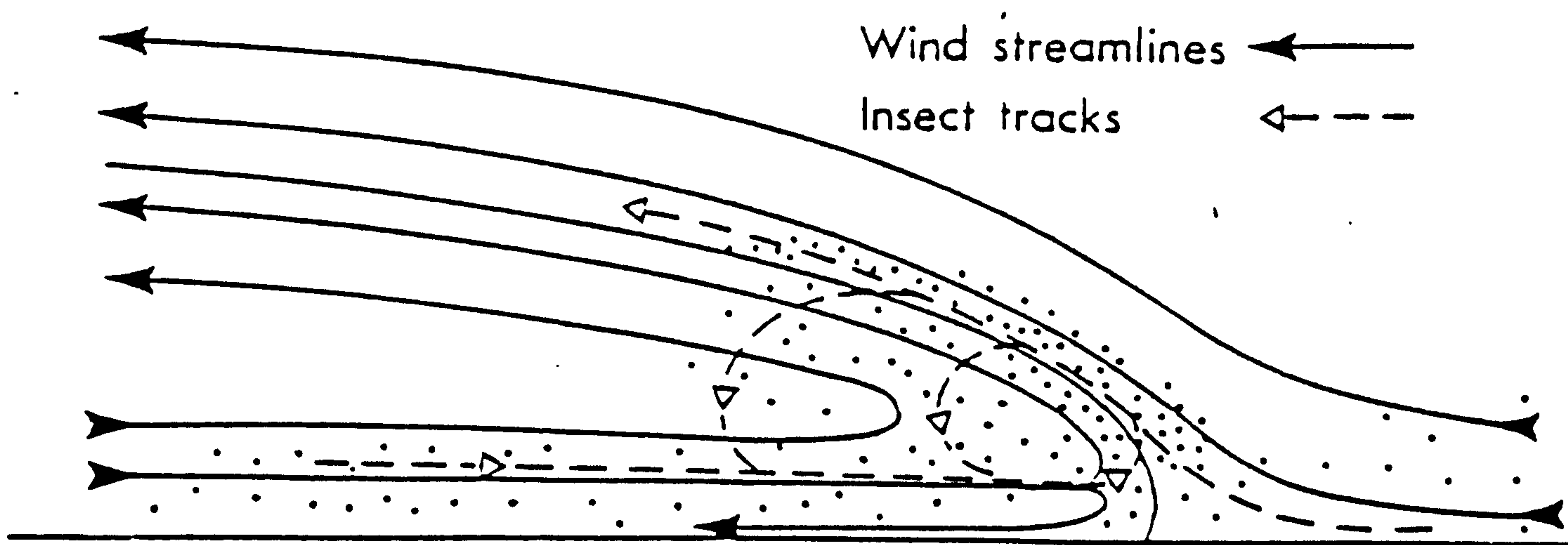


Figure 5. Windflow and insect tracks in the nose of a rainstorm outflow as shown by a schematic vertical section through an outflow crossing a radar site near Lukenya Hill, Kenya at about 1900, 29 February 1980 (from Pedgley et al (1982)).

It is not known how often topographically induced windfield disturbances concentrate flying armyworm moths, but such concentrations are likely to occur in relatively fixed locations in relation to topography and wind direction eg. west of the Kikuyu escarpment, Kenya. Rainstorm occurrence is more unpredictable, requiring regular monitoring if locations for possible armyworm concentrations are to be identified.

(e) The effects of temperature on African armyworm distribution and development rates.

As insects are poikilothermic (having body temperatures that vary with the surrounding temperatures), air temperature is an important factor determining both distribution and development rate. Knowledge of the rate of armyworm development is needed to estimate timing of moth concentration, oviposition, damaging caterpillar outbreaks, pupation and moth emergence. Air temperature in eastern Africa varies mostly with altitude, with a mean environmental lapse rate (decrease with height) of about 6°C per 1000m. At any one location, air temperature varies with season and with cloud cover although, as is usual in the tropics, seasonal variations are usually small and are exceeded by diurnal temperature changes. For example the difference in mean monthly temperature between the hottest month (March) and the coolest (July) at Machakos in the Kenya highlands is 4°C, while the difference between the mean maximum monthly temperature and the mean minimum (which correspond closely to daily maxima and minima respectively) is 12.5°C (Kenya Meteorological department 1984).

Turning to the effect of air temperature on *Spodoptera exempta*, Hattingh (1941) found in the Transvaal, South Africa, that African armyworm could not be reared in the laboratory at temperatures of less than 65°F (18°C) and

this is likely to be about the minimum development threshold. In Kenya, the 18°C mean daily isotherm lies at about 2,000m in most months and this does appear to be the maximum altitude at which outbreaks usually occur. Although there is little published on a maximum development threshold, Hattingh (1941) found that mortality increased rapidly at air temperatures of greater than 32°C.

The most detailed study of development rates in the field in eastern Africa (by W W Page published in Pedgley *et al* 1989) produced a linear regression of head capsule width (or instar) against number of days after moth concentration (taken as three days before first oviposition) (Figure 6) based on field data from the Machakos area at an altitude of about 1500m. It gave a development time, from first oviposition to moth emergence, of 36 days which agreed with earlier unpublished estimates for the Nairobi area (as used by Tucker & Pedgley 1983). Because of site-specific variations in development rate, especially due to shading and cloud cover, there are error terms averaging +/- 5 days attached to this regression. It is generally considered that Page's regression can be used for outbreaks at altitudes from about 1,200 to 2,000m, but outbreaks at lower altitudes often develop more rapidly (Rose 1975, Persson 1981, W W Page & C F Dewhurst unpublished). Both Rose (1975) and Persson (1981) found development periods, from oviposition to moth emergence, of about 30 days at altitudes of about 1,000m, and Persson found a development period of 23 days on the Kenya coast. Persson also reared *Spodoptera exempta* in Nairobi where, over a year, he found a mean total development period of 55 days, far longer than other estimates. This was caused by very long development periods (of 77 days) in June, July and August when armyworm outbreaks are not usually present and when mean

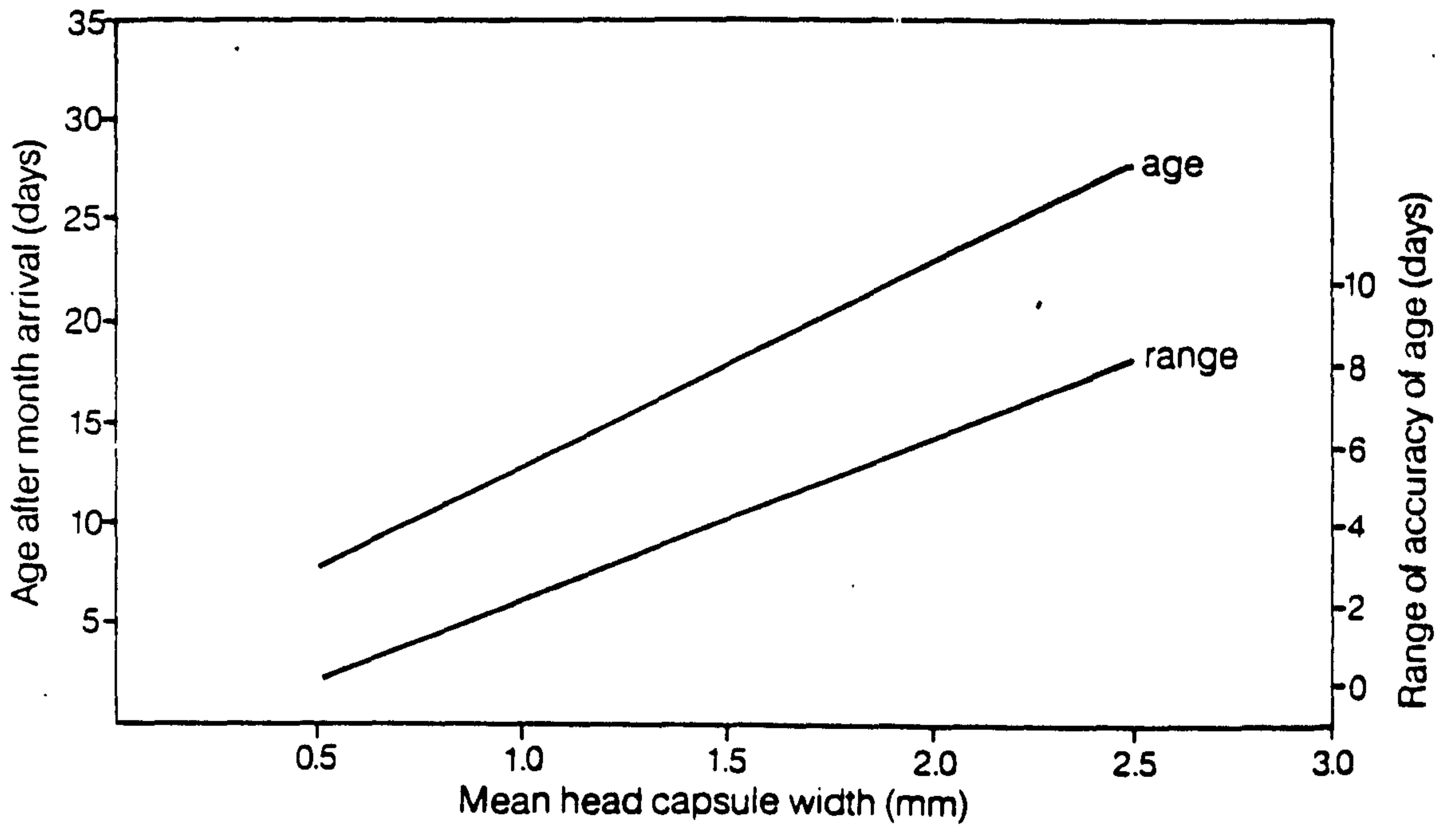


Figure 6. African armyworm larval head capsule width compared with time after moth arrival leading to oviposition (from Pedgley et al 1989)

air temperatures are 16°C, compared with 18°C for the rest of the year. It was not, however as long as Hattingh's (1941) figure of 82 days for *Spodoptera exempta* in a laboratory at a temperature of 18°C in Transvaal. Near the lower air temperature threshold, therefore, armyworm development rates decrease rapidly as mortality rates rapidly increase.

More recently Robinson (1991) used published analyses to develop a day-degree model to estimate durations of egg, larval and pupal stages of *Spodoptera exempta* at different mean monthly temperatures. He estimated mean temperatures, and hence *Spodoptera exempta* development times, for any given latitude and longitude in Kenya and Tanzania from a digital elevation model of the two countries. Armyworm development times were estimated automatically using a program 'Worms.exe'. The development equations were:

$$\text{Eggs: } d = 25.4 / (T - 14.4)$$

$$\text{Larvae: } d = 303.0 / (T - 6.7)$$

$$\text{Pupae: } d = 158.3 / (T - 10.2)$$

For comparison with previous estimates these give total development periods of 26 days at 27°C, 32 days at 24°C and 43 days at 20°C, where these are the mean monthly temperatures from January to May at Malindi (on the coast), Makindu (at 1000m) and Nairobi (at 1700m). These durations are close to previous estimates, except for Nairobi for where they are considerably longer, due to the inclusion of Persson's and Hattingh's data.

From comparison between the spatial variation in mean monthly temperatures and the distribution of armyworm outbreaks, Robinson considered that 27°C was likely to be close to an upper temperature threshold for *Spodoptera exempta* development and that high temperatures restricted the development of outbreaks on the Indian Ocean coast from December to April. The probable role of an upper

limit in restricting the occurrence of African armyworm in Sudan and the Sudano-sahel zone of west Africa has already been mentioned (P 21).

CHAPTER 3. DATA.

(a) African armyworm data

The area covered by this study was determined by the countries covered by the Regional Armyworm Forecasting Service, run by the Desert Locust Control Organization for Eastern Africa (DLCO-EA), Nairobi, which are Kenya, Tanzania, Uganda, Somalia and Ethiopia. This constitutes a well-defined area subject to the frequent occurrence of *Spodoptera exempta* outbreaks and is limited to the west by hot plains of Sudan and equatorial forest of Zaire. In the south the boundary is less distinct, judging by previous work that has identified some exchange of armyworm populations with those in Malawi, Zambia and further south (Rainey 1989) and by genetic studies that suggest that armyworm populations are closely related throughout eastern and southern Africa (Den Boer 1978). Data for Malawi and Zambia were occasionally available in Kenya but were too patchy for inclusion except for the few occasions when migration into southern Tanzania were indicated. The study generally covered the well-defined geographical region of eastern Africa for which most armyworm data were available.

Regular African armyworm reporting has been established for about thirty years in Kenya and Tanzania, but has been more irregular in the rest of eastern Africa. Reports of *Spodoptera exempta* outbreaks and moth catches, in light and pheromone traps, are sent to the national plant protection services of Ethiopia, Kenya, Somalia, Tanzania and Uganda. Reports are used by the national armyworm forecasting services in Kenya and Tanzania and by the Regional Armyworm Forecasting Service.

Spodoptera exempta data for 1972 to 1988 were extracted from records at DLCO-EA, the Kenyan Armyworm Forecasting

Service (previously the Regional Service) at the National Agricultural Research Centre (NARC), Muguga, the Tanzanian Armyworm Forecasting Service and the Ethiopian Ministry of Agriculture. These data consisted of reports of *Spodoptera exempta* outbreaks from farmers and district agricultural officers, together with data from special surveys in Kenya and Tanzania after 1978.

There were likely to be some differences in consistency between countries in the reports available to the study. As the study was based in Kenya and reporting procedure is well established there, it is likely that most damaging outbreaks in cropping areas were reported. However density of reports did, in part, reflect the density of human population and outbreaks in thinly populated pastoral areas were probably under-reported. Tanzania also has a well established reporting procedure but the availability of the reports at DLCO-EA, Nairobi was variable. In the best reporting years, 1986-87 and 1987-88, regular reports were supplemented by extra data collected by the Tanzanian Forecasting Service, whereas for some other years (eg 1980-81) there is evidence that data available to the study were incomplete. Evidence on the completeness of available data is discussed in the seasonal summaries. Ethiopian data was almost certainly incomplete, but there was no available evidence to suggest how many outbreaks were missed. Only outbreaks in southern Ethiopia (south of 10°N) were analysed.

Reports also included light and pheromone trap data from nationally coordinated networks of traps that recorded nightly moth catches in each country. Some light trap data were available for all years of the study. Pheromone trap data were available from 1978, following the development of an artificial female sex-attractant pheromone (Campion et al 1976). From 1982 there were additional pheromone trap data from local networks

installed in areas where primary outbreaks often occur. The present study used both original records and trap and outbreak data that were, at the time of data extraction, being entered into a computerized armyworm database on DBase 4 called 'Wormbase' (Day 1991). This database is available at the Armyworm forecasting centres in Kenya and Tanzania.

Control measures against armyworm outbreaks were sometimes reported, but these data were not used because there was no information on the effectiveness of control. Crop loss data were generally not available for individual outbreaks during the period of study. There were almost no data on the occurrence of low-density populations of *Spodoptera exempta*.

For each *Spodoptera exempta* season (October to July), outbreaks were tabulated chronologically and by district, including date, location, instar (or head-capsule width) of caterpillars, size and density of the outbreak, host plant, damage assessment, caterpillar mortality and control. For a few seasons it was possible to obtain such tabulations directly from 'Wormbase'. Outbreak locations were plotted on outline maps of eastern Africa, which were used together with daily synoptic windflow maps as the basis for trajectory analyses (Chapter 4). Outbreaks were also plotted on a degree-square basis for seasonal summaries (Appendix). Final maps for presentation were plotted using 'Mapics' computer mapping software.

(b) Weather data

Synoptic surface winds, required to estimate moth migrations, were obtained from daily windflow charts from the Kenya Meteorological Department (available at NARC) and the Meteorological Services of Ethiopia, Kenya and Tanzania. Winds were not estimated from atmospheric

pressure analyses (as done for northern Europe, Mikkola & Salmensuu 1965) because, near the equator, the geostrophic approximation, that winds above the friction layer are parallel to the isobars, does not hold. Moreover, pressure gradients near the equator are usually small. There are also problems in estimating windfields directly from wind observations. Surface winds (measured at 10 metres) are affected by friction, especially at night when temperature inversions prevent convective mixing, resulting in a shallow layer of very light winds. Night-time surface winds are, therefore, not representative of winds at the height of moth migration (e.g. 200-400 metres, Riley *et al* 1983). Unfortunately, upper air data were inadequate to define windfields at these heights. Daytime (1200 or 1500 LT) surface winds were therefore used on the basis that convective mixing makes them reasonably representative of winds up to several hundred metres, and that, in an area where synoptic-scale disturbances are infrequent, winds above the surface are not likely to change dramatically from the afternoon to the following night. The exception to this is when rainstorms are present, as these can result in dramatic mesoscale wind changes over a few hours. Trajectories were, in any case, terminated in the vicinity of rainstorms because moths were then likely to land (see P 40).

The Kenya Meteorological Department charts included station data on winds and rainfall occurrence, and rough, working, windfield analyses. The data were extracted and the windfields reanalysed manually to give wind streamlines suitable for trajectory analysis, using the streamline-isotach method described by Palmer *et al* (1955) and Barry & Perry (1973). Streamlines were drawn as continuous, usually curved lines, parallel to station wind arrows (but ignoring stations with rainfall) according to a set of conventions. Thus streamlines

could be parallel, diffluent or confluent, cyclonic, anticyclonic or associated with a neutral point (calm conditions). Wind speeds were plotted as separate isotach lines, which define areas of equal wind speeds.

Daily, weekly and monthly rainfall data were obtained from the Meteorological Services of Ethiopia, Kenya and Tanzania and from NARC, Muguga. Monthly rainfall totals were obtained for all seasons, from synoptic weather stations in Kenya and Tanzania. Weekly data were available from NARC for Kenya, for most armyworm seasons. Daily 24 hour rainfall totals, usually for the whole season but sometimes for shorter periods, were obtained for rain gauges within about 50 km of outbreak sites for all early season armyworm outbreaks and for some later ones. Night-time only rainfall totals were not available but, as discussed on p 40, for most places in east Africa, heavy 24 hour total rainfall amounts are a good indication of a late afternoon or evening rainstorm. The density of rain gauges varies greatly across east Africa, but data were usually obtainable for at least five gauges in each area. These were tabulated as space/time sections (see eg Table 18).

Daily rain-gauge records for Kenya were obtained as print-out from the Kenya Meteorological Department computer database and were more readily available for a large number of gauges than for Tanzania or Ethiopia. When rain gauge data were available for ten or more gauges near outbreak sites in Kenya, more detailed spatial analysis of rainfall distribution in relation to outbreaks could be carried out.

Data on the distribution of rainstorms from Meteosat infra-red satellite imagery were available from a secondary receiver at the Natural Resources Institute from October 1986 but the low resolution (about 30km) and

lack of calibration meant that they were not suitable for inclusion in this study. Higher resolution, calibrated (primary) data were available at NRI from October 1988 and at DLCO-EA, Nairobi from January 1989. This was after the main period used for this study, but an additional small study was later carried out using Meteosat data in relation to African armyworm outbreaks, for October 1992 to January 1993 .

c) Location data

Locations of outbreak sites, rain gauges and towns were checked on 1:1000000 scale road maps of Kenya and Tanzania and a 1:2000000 scale map of Ethiopia, and also in official gazeteers (United States Board on Geographical Names 1964) and were plotted on working overlays. Locations of meteorological stations and rain gauges were obtained from published and unpublished lists from the country Meteorological Services. Locations of places mentioned in the text are shown in Figure 1. The location of rainstorms from satellite imagery is discussed in Chapter 7.

CHAPTER 4. CLASSIFICATION OF OUTBREAKS AND SEASONAL SUMMARIES

(a) Introduction

Spodoptera exempta outbreaks were classified, based on Rose *et al* (1987) and Pedgley *et al* (1989) and as described in Chapter 1, into:

primary outbreaks - when parent moths were likely to have come from low density populations;

secondary outbreaks - when parent moths were likely to have come from previous outbreak populations;

critical outbreaks - outbreaks which, if left uncontrolled, would lead to many secondary outbreaks occurring in cultivated areas, following downwind migration. Critical outbreaks are those that must be identified for the success of the technique of 'strategic control', which aims to prevent subsequent outbreaks which are likely to cause economically important damage to cereal crops.

There is some ambiguity in Rose *et al* (1987) as to whether, by definition, primary outbreaks only occur at the beginning of the season. If they were so defined, it must be assumed that all outbreaks later in the season must come from previous outbreaks. Since one of the aims of this study was to determine whether or not this was the case in the seasons studied, the broader definition of 'primary outbreaks' given above was used. Primary outbreaks were further categorised as 'early' with estimated moth arrival from October to December, and 'late', from January to May.

In this chapter the overall frequencies of primary and secondary outbreaks are summarized, as deduced from development periods and trajectory analyses assuming that moths flew downwind. Then primary outbreaks are described by their main areas of occurrence, together with the weather associated with them. Secondary outbreaks are listed under the area of their source outbreaks, thus emphasising the direction and spread of outbreaks, from the primary outbreak areas. References are made to specific seasons as summarised in the Appendix (see below).

Critical outbreaks could sometimes be identified in the description of individual seasons but further analysis was needed. Analyses of migrations between outbreaks for all 16 seasons were used to assess frequencies of sources and destinations and to identify, quantitatively, areas where 'critical' outbreaks most frequently occurred. These areas are, therefore, those where monitoring should be concentrated in future seasons and where 'strategic' control measures are most likely to be successful.

The relative importance of outbreaks and low-density populations in African armyworm population dynamics is then discussed.

Forecasting the development of African armyworm outbreaks can be helped considerably by referring to previous similar seasons to find analogues. Summary descriptions of each of the 16 armyworm seasons analysed in the present study are included in the Appendix and these provide reference data and analyses relevant to the present chapter. They have also been published separately as a Technical Bulletin (Tucker 1993) for use by armyworm forecasters.

(b) Methods

Classification of outbreaks depended on estimates of the timing of 'moth arrival' prior to oviposition, the timing of moth emergence, and on moth migration trajectories. The available data have been described in Chapter 2. The methods of analysis of these data will now be described.

(i) Outbreaks

For each African armyworm outbreak, the timing of moth arrival and concentration immediately preceding oviposition was estimated, taking account of development rates. As described in Chapter 2, the development rate of *Spodoptera exempta* depends on temperature and, therefore, altitude. For all outbreaks above 1200m, W. W. Page's regression of head capsule width (or instar) against number of days after 'moth arrival' (taken as three days before first oviposition) was used (Pedgley et al. 1989). This gives a development time from first oviposition to moth emergence of 36 days. Total development rates for outbreaks at lower altitudes were assumed to vary from 23 days on the coast to 30 days at 1000m (Rose 1975, Persson 1981). Oviposition or moth arrival dates and moth emergence dates were estimated by tables developed by Betts (unpublished, Table 4). From these tables, total development periods for intermediate altitudes could be estimated using the regression

$$d = 0.84e + 22.6$$

where d = development period from oviposition to adult and e = elevation in 100 metres.

Robinson's (1991) development period estimation based on day-degree and digital elevation models (Chapter 2) does not give estimates for different instars (or head capsule widths) and was not available when the present work was started, so has not been used.

ALTITUDE 1000M			COAST		
DAYS FROM OVIPOSITION	INSTAR	DAYS TO EMERGENCE	DAYS FROM OVIPOSITION	INSTAR	DAYS TO EMERGENCE
	EGG			EGG	
3	1	27	2	1	20
6	2	24	5	2	18
8	3	22	6	3	16
10	4	20	8	4	15
12	5	18	9	5	13
15	6	15	12	6	11
20	PUPA	10	16	PUPA	7
30	MOTH	0	23	MOTH	0

Table 4. Mean duration of *Spodoptera exempta* life-history stages at about 1000m altitude and on the coast in eastern Africa.

Gregarious *Spodoptera exempta* caterpillars are usually reported after they turn black in the fourth instar (Pedgley et al 1989) so, when the caterpillar age was not reported, they were assumed to be in IV-VI instars. 'Moth arrival', as used in Pedgley et al (1989), defines the timing of outbreaks in the following account, unless stated otherwise.

(ii) Trap catches

Pheromone and light traps were used to monitor moth influx. Light traps attract moths and other insects due to the disruption of other directional cues. Catching efficiency varies with moon phase and cloudiness because the moon acts in competition to affect moth behaviour (Bowden 1973, 1982, Bowden & Church 1973, Douthwaite 1978). Catches, therefore, usually decline with increasing intensity of moonlight and are highest at new moon or on cloudy nights and lowest on clear nights with a full moon. The exceptions are where moths have been found to fly preferentially at particular moon phases. Because of this variation in catch, only five-fold increases or more in catch from one night to the next were taken to indicate moth influx. The same criterion was applied to catches from pheromone traps. A large increase in light-trap catch within an estimated moth arrival period was taken as evidence for immigration on that night, while a large increase in pheromone-trap catch (often up to 4 days later) was evidence of synchronous mating by large numbers of moths. Large increases which occurred outside estimated moth arrival periods for known outbreaks, were taken to indicate the likely presence of unreported outbreaks, or of moths emigrating or in transit from such outbreaks. A long sequence of small catches suggested a persistent low density population.

(iii) Rainstorms

The association between rainstorms and *Spodoptera exempta* outbreaks, caused by parent moths being concentrated by gust fronts (Pedgley et al. 1982, Tucker & Pedgley 1983 and Pedgley et al. 1989 and described in Chapter 2), was used to help refine estimated moth arrival dates. Days with rainstorms (defined as those with >10mm rain) were plotted for gauges which lay within about 50km of the outbreak site. When rainstorms occurred at or near the outbreak site during the estimated moth arrival period, it was assumed that parent moths were concentrated on these days.

(iv) Trajectory analysis

As described in Chapter 1, trajectories of insect migrations have been calculated from weather data for many years, using the assumption that the particular insect species was likely either to fly in a downwind direction or to be carried downwind because windspeeds usually exceeded the insects' flying speed (eg Mikkola & Salmensuu 1965).

Recent work on insect migration in the USA has used air parcel trajectories that are calculated on a regular basis from National Weather Service computer models (Scott & Achtemeier 1987, Hutchins et al 1988, McCorcle & Fast 1989, Showers et al 1989, Smelser et al 1991). These trajectories were available for surface winds and for 850hPa and 700hPa pressure surfaces, and for two 12-hour segments ending at 0600 and 1800 local time for designated end points in the USA. In the present study such computerised trajectories were not available and, although it would have been feasible to develop a simple computer model based on subjectively analysed windflow charts (as was done by Tucker 1976), the work involved in

entering weather data into the computer did not justify the expenditure of time. Trajectories to estimate likely moth migrations and to investigate links between outbreaks were, therefore, calculated, as objectively as possible, graphically using transparent overlays to trace wind streamlines from a series of windfield analyses covering the period of estimated migration.

Possible sources of moths giving rise to outbreaks were estimated by backtracking for nights within likely moth arrival periods, and possible destinations by forward tracking from estimated moth emergence dates. Both backtracks and forward tracks gave estimates of likely migration routes. One surface windflow map was used for each night's migration and movement was assumed to be downwind at the daytime surface wind speed and direction, as discussed on page 61 and by Tucker et al (1982) and Tucker (1984a). Moths were assumed to fly for 10 hours a night as a rough upper estimate, based on observations that moths take off at dusk from daytime refuges or later in the evening after emergence, and that moth landing takes place mainly at dawn (Rose & Dewhurst 1979, Riley et al 1983).

Trajectories were then calculated for two five-hour segments for each night, representing the periods from after dusk to midnight and from midnight to dawn respectively. They were drawn along the wind streamline for a distance determined by the wind speed at the midpoint of the segment, according to the formula:

$$D = W.T.M^{-1}$$

where D = Distance on map (cm)

W = Windspeed (converted to kilometres per hour)

T = Time represented by one segment (hours)

M = Map scale (kms.cm⁻¹)

(see e.g. Fig 7).

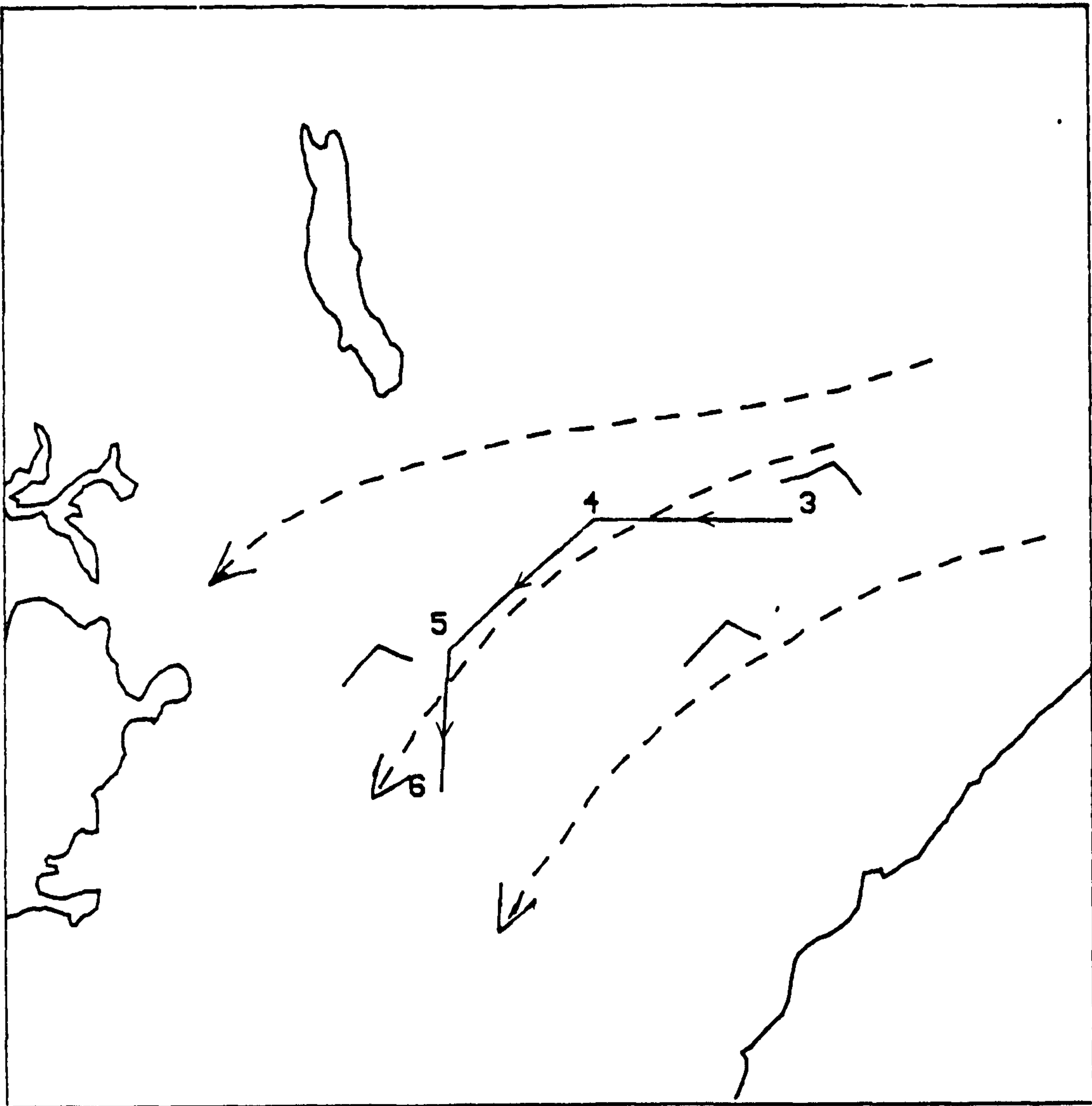


Figure 7. Construction of back trajectories of likely moth movement from a wind streamline analysis. The trajectory is the continuous line and the numbers are dates at 00LT. Wind streamlines for 1500LT on the 4th are dashed. Station wind arrows indicate wind speeds of 5m/s. The length of a trajectory segment equals windspeed times duration e.g. $5\text{m/s (18km/h)} \times 10\text{h} = 180\text{km}$.

The total duration of moth flight varies with the length of the pre-reproductive period and the flight capacity of the individual moths (Page 1988, Parker & Gatehouse 1985 a,b). The maximum number of nights' migration was assumed to be four, assuming migration occurred during the pre-reproductive period and based on information available when the study was started, but backtracks were ended before this if they came from known earlier outbreaks or from the coast. Similarly forward tracks were ended after four nights or if they entered a zone of light, variable winds such as those associated with synoptic-scale convergence. Although recent work (Wilson & Gatehouse 1993) has shown that the pre-reproductive period can be up to seven nights and, exceptionally, up to 13 nights in females, median values were between one and three nights. Furthermore errors involved in calculating trajectories increase rapidly with their length. Tucker (1984) estimated that for each trajectory segment, errors of up to 20° in direction were possible, since wind arrows are only plotted to an accuracy of 10° and additional errors would be introduced in interpolating between stations. An error of 20° accumulated over two nights at a wind speed of 12.5 km.h^{-1} gives an end point 100km from the correct position for a trajectory length of 300km (from the cosine formula). In disturbed windflows direction errors could be larger but since large-scale winds associated with disturbances tend to be light over eastern Africa, the distance errors would be reduced. In general, because of the increase in error with increased length, it was not considered reasonable to extend trajectories beyond 4 nights.

Estimates of armyworm moth arrival (for backtracks) and moth emergence (for forward tracks) usually have errors of about +/- 5 days so trajectories were calculated for about 10 days for each outbreak. As demonstrated in Tucker (1984) backtrack sources can be very scattered

when winds are variable and the same applies to forward trajectories.

Because of these various sources of error, individual trajectories were used only as indicators of likely migrations rather than precise predictions. The area covered by all the backtracks (or forward tracks) associated with a particular armyworm outbreak, however, could be assumed, with some degree of confidence, to define the total possible source (or destination area). In the case of backtracks, when there were no known outbreaks in this broad source area with emergence dates approximating to the migration dates, then the outbreak was classified as primary. When there were such potential source outbreaks the candidate outbreak was classified as secondary.

The analyses were carried out for October to April in each season. From April onwards, overlapping generations made further analysis impossible except when new outbreaks occurred in regions or countries previously reported clear, e.g. in Ethiopia, usually in April or May.

(v) Seasonal summaries

The distributions of primary and secondary outbreaks were mapped by degree square for each season from 1972-73 to 1987-88. Migrations between outbreaks, from trajectory analyses, were indicated by arrows between the appropriate degree squares. These maps, together with the original tabulated outbreak data, and trajectory and rainfall analyses, were used as the basis of the summary descriptions for each season (see Appendix). For presentational reasons, the maps shown in the seasonal summaries were simplified by showing only the month in which the first outbreak occurred in that degree square.

Distributions of primary and secondary outbreaks and the effects of weather on the development of each season were examined. The seasonal summaries are referred to in the following classification of outbreaks, to provide examples and to avoid repetition of descriptions that would otherwise be necessary in presenting the large amount of analysed data.

(vi) Source/destination matrices

The original degree square maps showing all outbreaks (or groups of outbreaks) and migration links between outbreaks, deduced from trajectories, were used to determine frequencies of sources and destinations for 1972-88, to establish the most frequent locations of critical outbreaks and to determine frequencies of particular migrations between outbreaks. These frequencies were summarized on two matrices of sources versus destinations, one for the months October to December and the other for January to July, where these were the months of 'moth arrival' leading to the source outbreaks. The number of degree squares in the area 6°N to 12°S and 30 to 42°E is 216 but most had too few outbreak occurrences over the 16 year period for meaningful frequency analysis. The data were therefore aggregated into 2° * 2° squares and the area covered was reduced slightly to 6°N to 10°S and 32 to 40°E. This cut out the most western areas, where there were very few cases, the most eastern area which, south of 2°S, is mostly sea, and southern Tanzania, which, it was found, is seldom a source area for outbreaks further north (p 73).

Results and Discussion.

(i) Trajectory analyses

There were far too many trajectories constructed to present them all in this thesis. Particular examples are presented in the Appendix and are referred to in the present section.

For the rest of this chapter, the results of the trajectory analyses are used, together with rain gauge data and more general analysis of daily surface windfields, to describe likely sources of African armyworm outbreaks and to classify them into 'primary' or 'secondary' outbreaks. Backtracks and forward tracks showed that most moth migrations occurred on winds that were close to the seasonal dominant windflow ie migrations towards the west from October to March (Figures 9-11) and to the north-west or north from April to June (Figure 14). It has therefore been possible to summarise the development of primary and secondary outbreaks and migrations between them by area, referring to individual trajectory analyses as examples and when they differ from the dominant pattern.

(ii) Overview

A brief overview is included to help the reader put the following descriptions of primary and secondary outbreaks, and the individual season analyses included in the Appendix, into context.

First outbreaks of the season in Kenya and Tanzania were nearly all primary, the exceptions resulting from moths migrating from southern Somalia to Kenya in three seasons and from Malawi to southern Tanzania in one season.

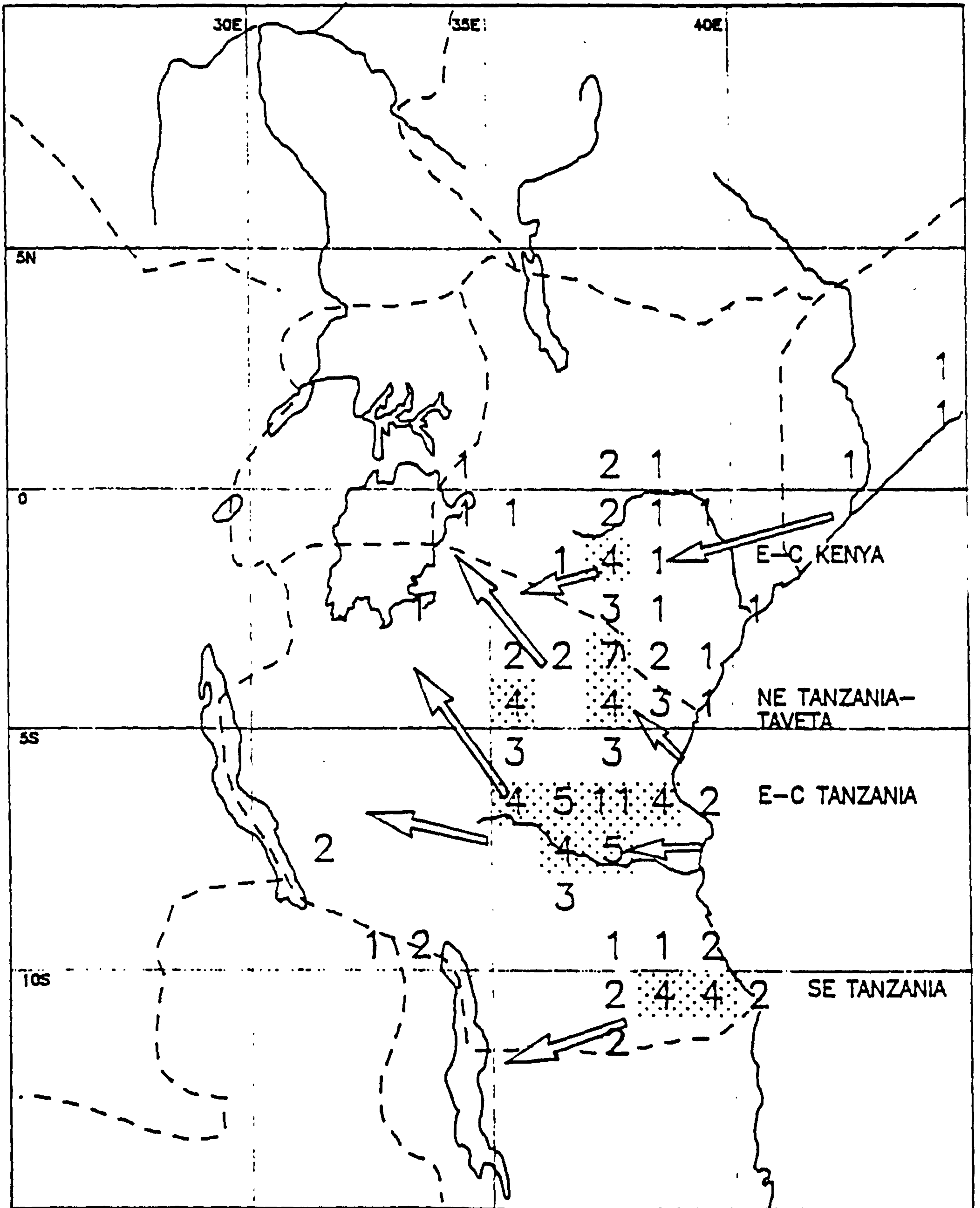
There were no examples of southward moth migration from Ethiopia to Kenya.

Early primary outbreaks occurred most frequently in east-central Tanzania (thirteen seasons), north-east Tanzania and Taveta (nine seasons), south-east Tanzania (nine seasons) and east-central Kenya (seven seasons) (Fig. 8).

Most outbreaks later in the season could be backtracked to earlier outbreaks and so were secondary. In severe seasons, secondary outbreaks were far more numerous than primaries and occurred very widely across eastern Africa. Secondary outbreaks often resulted from cross-border migration, especially from Tanzania to Kenya and, later, from Kenya to Ethiopia.

Late primary outbreaks (not resulting from previous outbreaks) occurred in southern Ethiopia (five seasons), on the Kenya coast (four seasons), the Tanzania coast (four seasons), and in east-central Kenya (three seasons). Unusual late primaries occurred in western Kenya (one season) and east-central and north-east Tanzania (one season). Late primaries were taken as evidence of low-density armyworm populations persisting during the armyworm season and then being concentrated.

Figure 8. Frequency of early primary outbreaks (moth arrival October-December) 1972-1987 by degree square. Squares with primary outbreaks in more than 3 seasons are stippled and the directions of the main early season moth migrations to and from primary outbreaks are shown by broad arrows.



(iii) Primary outbreaks

The six main areas of early primary outbreaks are shown in Fig 8 and were, in order of importance:

East-Central Tanzania (Morogoro, 6-8°S 36-38°E, and Dodoma-Kondoa areas, 4-7°S 35-36°E)

Early primary armyworm outbreaks occurred in the Morogoro region in all but three seasons. Exceptions were two very low seasons (1972-73 and 1977-78) with no early primaries in Tanzania, and one (1973-74) when first outbreaks in the Morogoro area had moth arrival dates in early January. In four seasons, early primaries also occurred further west in an area from Dodoma north to Kondoa. No moth arrival dates were before the end of October. Winds were predominantly from the east or north-east, so sources were either local or near the coast, from Dar es Salaam north to Tanga (e.g. Fig 9). Most early primary outbreaks in the Morogoro and Dodoma regions were associated with the start of the main rains (1975-76, 1979-80, 1983-84 and 1984-85) or with isolated rainstorms preceding these rains (1976-77, 1987-88).

North-East Tanzania (and Taveta, Kenya) (3-6°S, 37-39°E)

Early primary outbreaks (moth arrival from November to early January) were reported in an area from Kilimanjaro eastwards to adjacent areas of Taveta, and southwards along the Pare and Usambara mountains, from Same to Korogwe and Handeni. Eight of the nine seasons in which they were reported were between 1978-79 and 1987-88. Backtracks from Taveta and adjacent areas of Kilimanjaro region usually came from the east, near the Kenya coast but those from west of the Pare-Usambara mountains came from the south-east due to the topographic deflection of the low-level winds (Figs 10,11). Primary outbreaks were

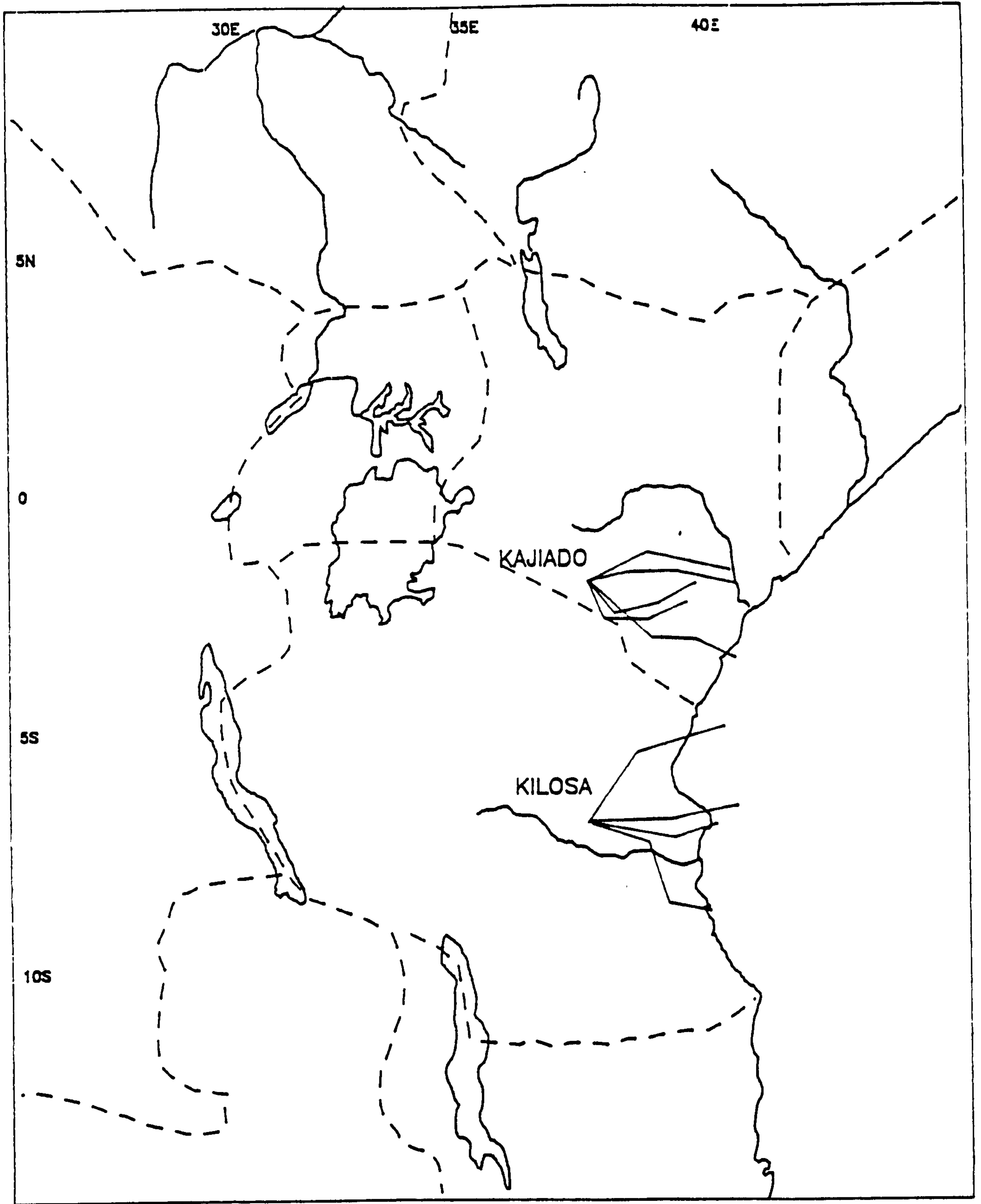


Figure 9. Backtracks from early primary outbreaks at Kajiado and Kilosa with moth arrival 6-23 November 1976.

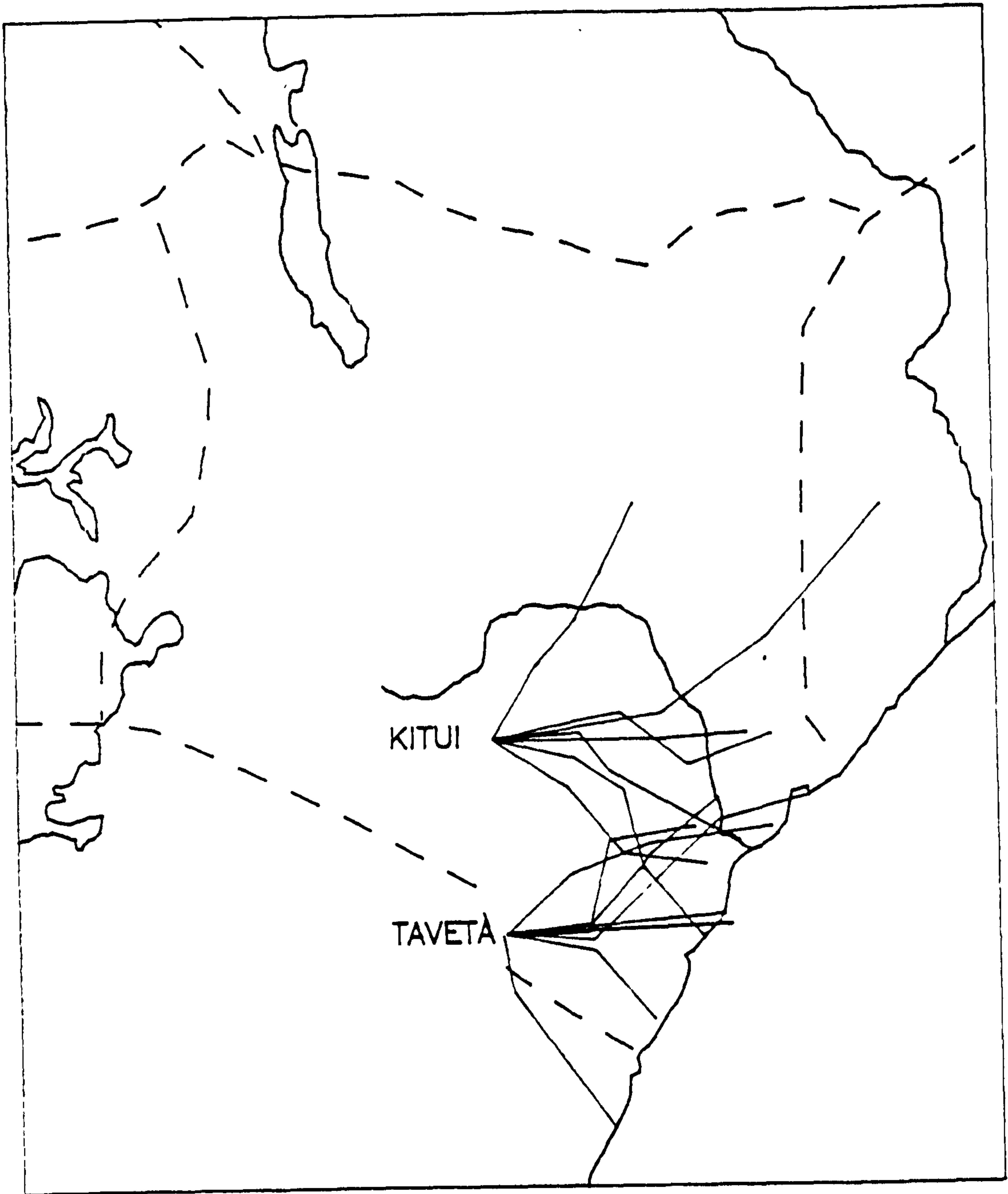


Figure 10. Backtracks from early primary outbreaks at Kitui and Taveta with moth arrival 6-20 November 1980.

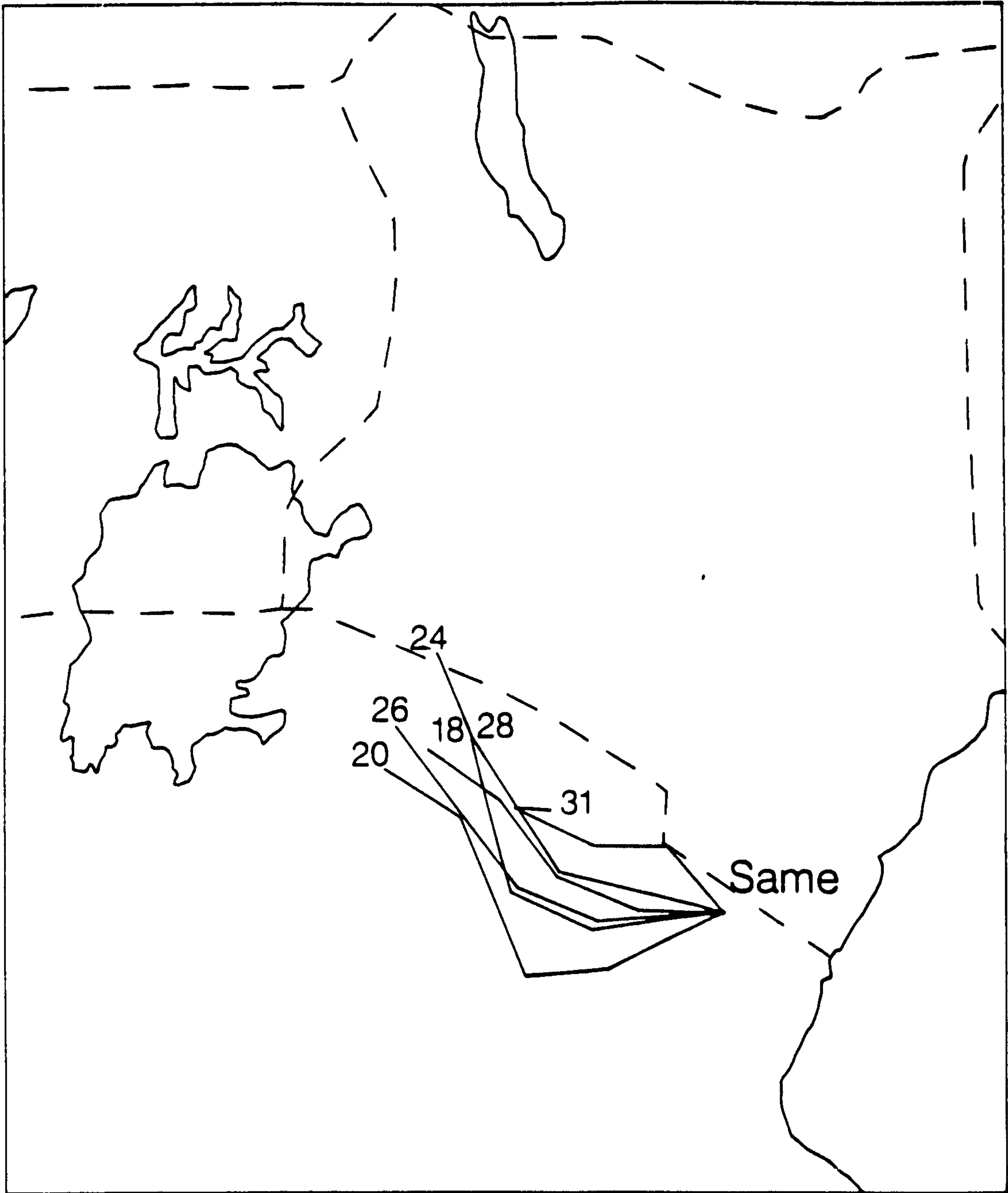


Figure 11. Forward tracks from primary outbreaks near Same with moth emergence 16-31 January 1982.

usually associated with rainstorms at the time of moth concentration (e.g. in mid-November of 1979-80, 1980-81, 1984-85 and 1985-86), at the start of, or during, the short rains.

South-east Tanzania (9-12°S 37-41°E)

Early primary armyworm outbreaks occurred from Mtwara inland to Tunduru in ten seasons, most frequently near Nachingwea. Estimated moth arrival dates were from the end of October to the end of December. After mid-October, surface winds were predominantly easterly or north-easterly so likely moth sources were in the eastern part of the Mtwara-Lindi area. Early primary outbreaks were often associated with late first rains (November 1986, December 1974, 1979, 1984) or with isolated early rainstorms three to four weeks before the main rains (October 1981, November 1983).

East-Central Kenya (0-3°S 37-38°E)

Early primary outbreaks occurred in the east-central Kenya highlands in six seasons (1976-77, 1978-79, 1980-81, 1983-84, 1984-85 and 1985-86), in an area from Meru (east of Mt Kenya) in the north to Kajiado in the south, and from Kitui in the east to Nairobi in the west.

In four seasons, primary outbreaks had estimated moth arrival dates in October or November, associated with the first rainstorm of the short rains, and in two, first reported outbreaks were in December, towards the end of the short rains. Backtracks were from eastern or south-eastern Kenya where sources were presumably low-density populations, since there were no reports of outbreaks there (e.g. Figs 9,10). Even after the onset of the north-east trade winds in November, no backtracks came from the direction of Ethiopia because winds were

consistently east of north-easterly. However, some came from the direction of Somalia where, in three years, there were earlier outbreaks (see below and p 71).

Late primary outbreaks occurred in this area in three seasons. In two, they were associated with several days of rainstorms in the usually dry month of January. Backtracks were from the east or north-east, while the only known earlier outbreaks were to the south. In one season (1973-74), a late primary outbreak occurred at Meru, associated with rainstorms in March at the beginning of the long rains. Backtracks were from the east or south-east while the only possible parent outbreaks were in the west (south Nyanza) or well south (in central Tanzania).

The Coasts of Central and Northern Tanzania, Kenya and Southern Somalia

On the central Tanzania coast early primary outbreaks occurred in seven seasons (1973-74, 1975-76, 1978-79, 1979-80, 1981-82, 1985-86 and 1987-88) all with estimated moth arrival in December. On the Kenya coast early primary outbreaks were reported near Mombasa in October 1980 and November 1985, and near Lamu in November 1985. On the coast of southern Somalia, early primary outbreaks were reported in November in three seasons (1978-79, 1980-81 and 1985-86).

As winds on the coast were predominantly onshore easterlies, sources of early outbreaks there were likely to be local although, in Somalia, moths could have come from the north-east along the coast.

For the same reason, late armyworm outbreaks on the coasts of Tanzania (in 1973-74, 1981-82 and 1983-84) and Kenya (in 1979-80, 1981-82, 1983-84 and 1987-88) were

probably primary. Outbreaks were associated with rainstorms following dry periods from January or February to March. Large outbreaks on the Kenya coast in April 1982 and April - May 1984 (when they covered more than 16000ha) were associated with the beginning of the long rains after very dry weather.

Southern Ethiopia

Primary armyworm outbreaks were reported with estimated moth arrival in mid-February or March from southern Ethiopia (Gamo Gofa or Sidamo) in five seasons (1978-79, 1981-82, 1984-85, 1985-86 and 1986-87). They followed a gap of at least 2.5 months, during the dry season, since the previous Ethiopian outbreaks. They were associated with early rainstorms at the beginning of the armyworm season in Ethiopia and were likely to have local sources because there were no southerly winds suitable for bringing moths from Kenya before April. Small catches of moths at Jinka from January to March indicated that armyworm can survive there in the dry season.

Other primary outbreaks

In three seasons, early primary outbreaks occurred in south-western Tanzania; in Mbeya region in November 1978 and 1986 and Rukwa region in November 1986 and September 1987.

In two seasons (1984-85 and 1986-87), early primary outbreaks occurred in western Kenya in October, and in November 1986 there was also an early primary in Mwanza region of north-western Tanzania.

Late primary outbreaks occurred in South Nyanza in February 1978 and in the Morogoro, Dar es Salaam and

Kilimanjaro areas in May 1973 in two very low armyworm seasons (see p20).

(iv) Secondary outbreaks

Secondary outbreaks could be backtracked through one or more generations to primary outbreaks, as described below in order of frequency.

Secondary outbreaks derived from Morogoro primary outbreaks

In most seasons primary outbreaks in the Morogoro area were followed by secondary outbreaks in an area from Dodoma to Singida, and sometimes as far west as Tabora, where moths usually arrived in December or January following westward migration on easterly or south-easterly winds. In many years there was a second generation of secondary outbreaks further northwest, from Shinyanga to the shores of Lake Victoria, and in southern Uganda (eg 1986-87, Fig 52). In four seasons (1973-74, 1975-76, 1976-77 and 1981-82) northward migration across Lake Victoria probably occurred, judging by outbreak distributions, trap catches and windfields (e.g. Fig 41). In each case, Uganda outbreaks occurred two months after those in the Morogoro area. Morogoro primary outbreaks were, therefore 'critical' for outbreaks both in central Tanzania and Uganda in these seasons.

Secondary outbreaks derived from north-east Tanzania-Taveta, Kenya primary outbreaks

In six seasons (1973-74, 1974-75, 1979-80, 1981-82, 1986-87 and 1987-88) trajectories indicated that moths migrated north-westwards from outbreaks in the Same to Handeni area to give secondary outbreaks in the Arusha - Kilimanjaro area. In three (or four) seasons (1981-82,

1986-87, 1987-88 and probably 1979-80) there were then several generations of outbreaks in the Arusha-Kilimanjaro area, from February to April or May, indicating persistent populations with moths flying relatively short distances (50km at most).

In six seasons (1975-76, 1976-77, 1978-79, 1979-80, 1986-87 and 1987-88), however, Arusha-Kilimanjaro was also a major source of moths flying at least 450km north-westwards to Nyanza and Western Provinces of Kenya, and possibly into eastern Uganda (figs 11,42,44). The persistent presence of low-level south-easterly winds in northern Tanzania enabled migration from Arusha-Kilimanjaro to western Kenya to take place throughout the season, although it usually occurred in January and February. The north-east Tanzania/Taveta area is therefore a 'critical' source area for secondaries in western Kenya.

Late outbreaks in north-east Tanzania and Taveta were important sources for many outbreaks in central Kenya, following the seasonal windshift from easterly or southeasterly to southerly. In 1974 and 1975, moth influx in central Kenya was indicated by very high catches of moths in light traps near Nairobi. Migration to southern Ethiopia may also have occurred on strong southerly winds, as from east-central Kenya and coastal Kenya (p 72).

In two seasons, 1981-82 and 1987-88, there was good evidence for migration from outbreaks in the Arusha-Kilimanjaro area to east-central Kenya in late March, associated with weather disturbances but before the seasonal windshift to south-easterly. Outbreaks, with no known sources in Kenya, were reported in Machakos district (in both seasons) and Kitui and Kajiado districts (in 1988 only). Moth arrival was associated

with widespread rainstorms and synoptic-scale windflow disturbances giving southerly or south-westerly winds over a period of several days at the end of March, with backtracks coming from northern Tanzania.

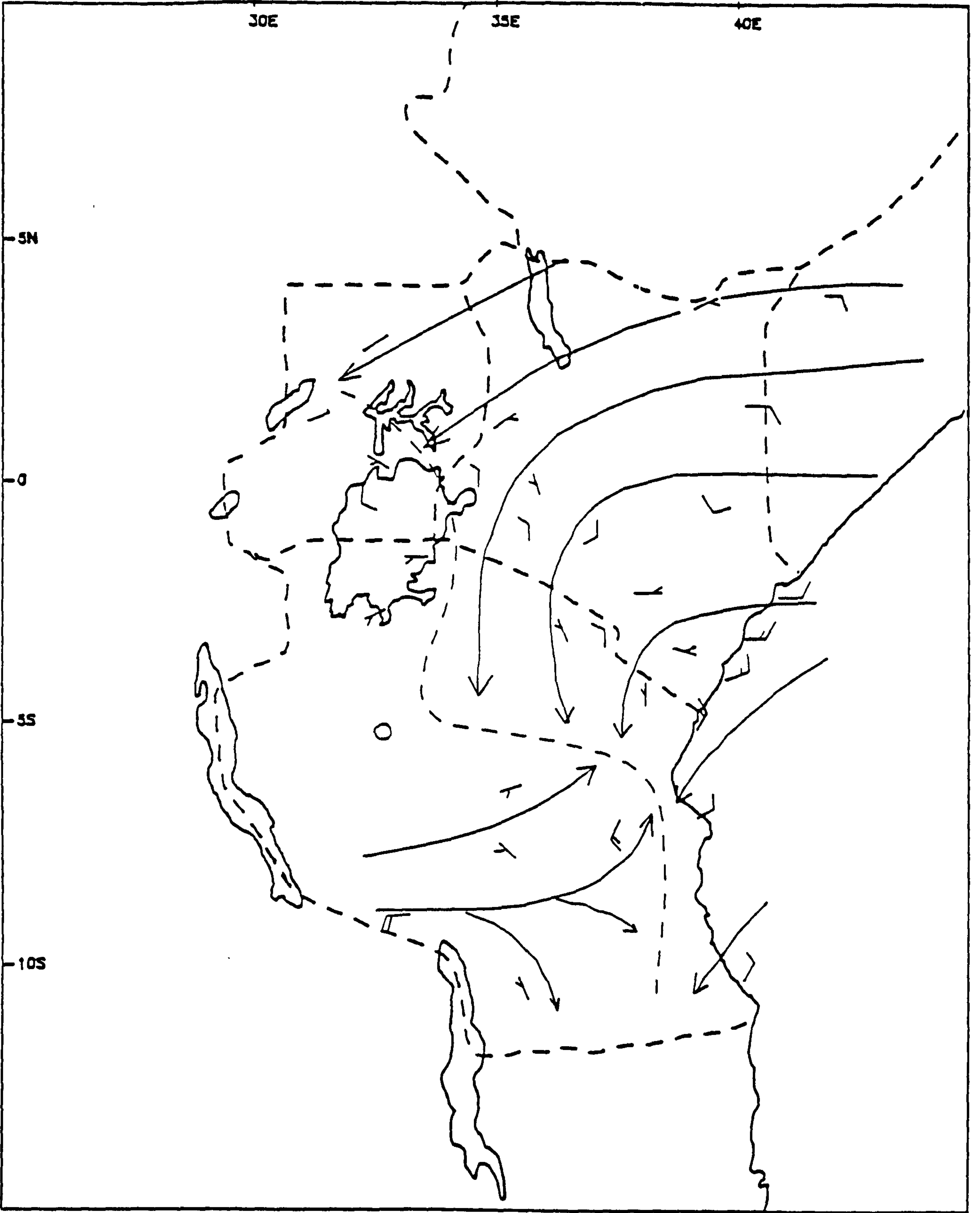
Secondary outbreaks derived from the east-central Kenya primary outbreaks

Primary outbreaks in east-central Kenya, with estimated moth arrival from October to January, generally gave rise to secondaries in central Kenya, following short moth migration to the west or southwest. In 1976-77 (Fig 42), however, an early primary outbreak in Kajiado was unusually far south and northerly winds (Fig 12) probably took moths from there to western Kilimanjaro district (north Tanzania) where outbreaks were reported in January.

In two seasons, 1980-81 and 1984-85, primary outbreaks near Meru gave rise to particularly large numbers of secondary outbreaks in central Kenya in November, following migration on north-easterly winds. In early December 1980, outbreaks were possibly supplemented by moth migration from south-east Kenya or southern Somalia. Secondary outbreaks in November and December 1984 were the most serious of the sixteen year period, and resulted from a combination of rainstorms and dry periods (following a drought) leading to a high rate of larval survival (Pedgley et al 1989).

In five seasons (1976-77, 1978-79, 1979-80, 1984-85 and 1985-86), moths emerging from secondary outbreaks in east-central Kenya migrated towards south Nyanza where there were outbreaks in January or February. These migrations were confirmed by high catches on one or two nights at Muguga light trap (just west of Nairobi) and, in three seasons (1976-77, 1978-79 and 1979-80), by the

Figure 12. Surface windfield 2 January 1977. Arrows are wind streamlines. The small arrows show wind directions and speeds (in 2.5 m.s^{-1} intervals) at weather stations. The broken line is a line of wind convergence.



occurrence of outbreaks near Magadi (in the Rift valley) on the predicted migration route. In December 1984, moths continued migrating to Burundi, judging by an unusual outbreak there (Pedgley et al 1989). Then very large source populations and unusually strong east to north-east winds, extending across Lake Victoria, could have resulted in enough moths surviving the long migration to form an outbreak.

In eight seasons, outbreak numbers increased in east-central Kenya from late March to May, due to local build-up and immigration from northern Tanzania. In these seasons, outbreaks also spread northwestwards to Nakuru, Eldoret and Kitale districts. In five seasons (1973-74, 1975-76, 1976-77, 1979-80 and 1978-88), outbreaks in southern Ethiopia in April and May possibly originated from moths migrating from east-central Kenya on strong southerly winds, with source outbreaks near Meru and/or Kitui. Migration northwards from outbreaks further west was unlikely because winds from Nairobi westwards tended to remain easterly or southeasterly throughout the long rains.

Secondary outbreaks derived from the coastal primary outbreaks

Primary outbreaks on the coast of southern Somalia in November of 1978 (Figure 13), 1980 and 1985 were possible sources for secondary outbreaks in east-central Kenya. Moths would have had to have flown about 2 m s^{-1} faster than the daytime surface windspeed to have completed the 1000km journey in four nights. In Tanzania, however, coast primaries did not give rise to first outbreaks downwind in the Morogoro area because they usually occurred at the same time as, or later than them.

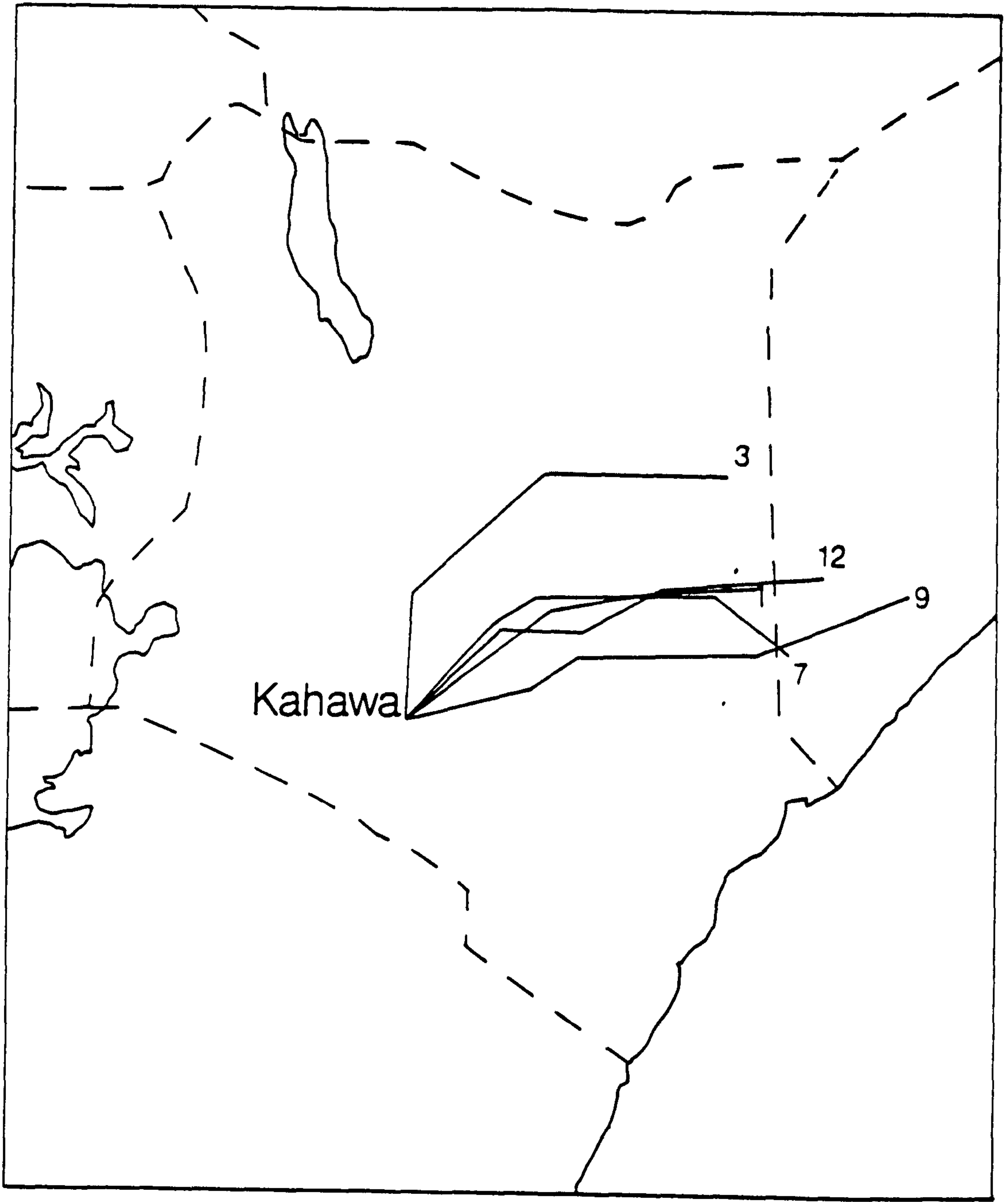


Figure 13. Backtracks from an outbreak at Kahawa (near Nairobi) with moth arrival 1-15 December 1978.

Late primary outbreaks on the Kenya coast in April 1982 and in April and May 1984 were probably sources of moths leading to outbreaks in Sidamo region of southern Ethiopia, as indicated by backtracks from Moyale (Fig 14). Backtracks in May 1984 showed that moths could have flown the 800 km in three or four nights, especially if moths flew in the low-level southerly jet stream that is known to occur over eastern Kenya from May to September at heights of above 500 m. Windspeeds in this jet are often 12 to 20 m s⁻¹ at 1000m (Findlater 1966, 1967, 1969). Further evidence for this large-scale northward movement was provided by the occurrence of secondary outbreaks in eastern and northern Kenya, on the Tana River and at Wajir, Marsabit and Mandera.

Secondary outbreaks from the southern Ethiopia primary outbreaks

Only the beginning of the main armyworm season in Ethiopia has been examined here. Most later outbreaks in Ethiopia and Yemen from June to August were likely to be secondary, derived from earlier outbreaks in Gamo Gofa, Sidamo or Harar provinces.

Outbreaks were reported from late September to early January in southern Ethiopia (Gamo Gofa or Sidamo) in five seasons (1978-79, 1983-84, 1984-85, 1986-87 and 1987-88) probably derived from earlier Ethiopian outbreaks. They were very unlikely to have given rise to outbreaks further south because winds were dominantly easterly, blowing towards southern Sudan where, however, no outbreaks have been reported from November to January (Haggis 1984).

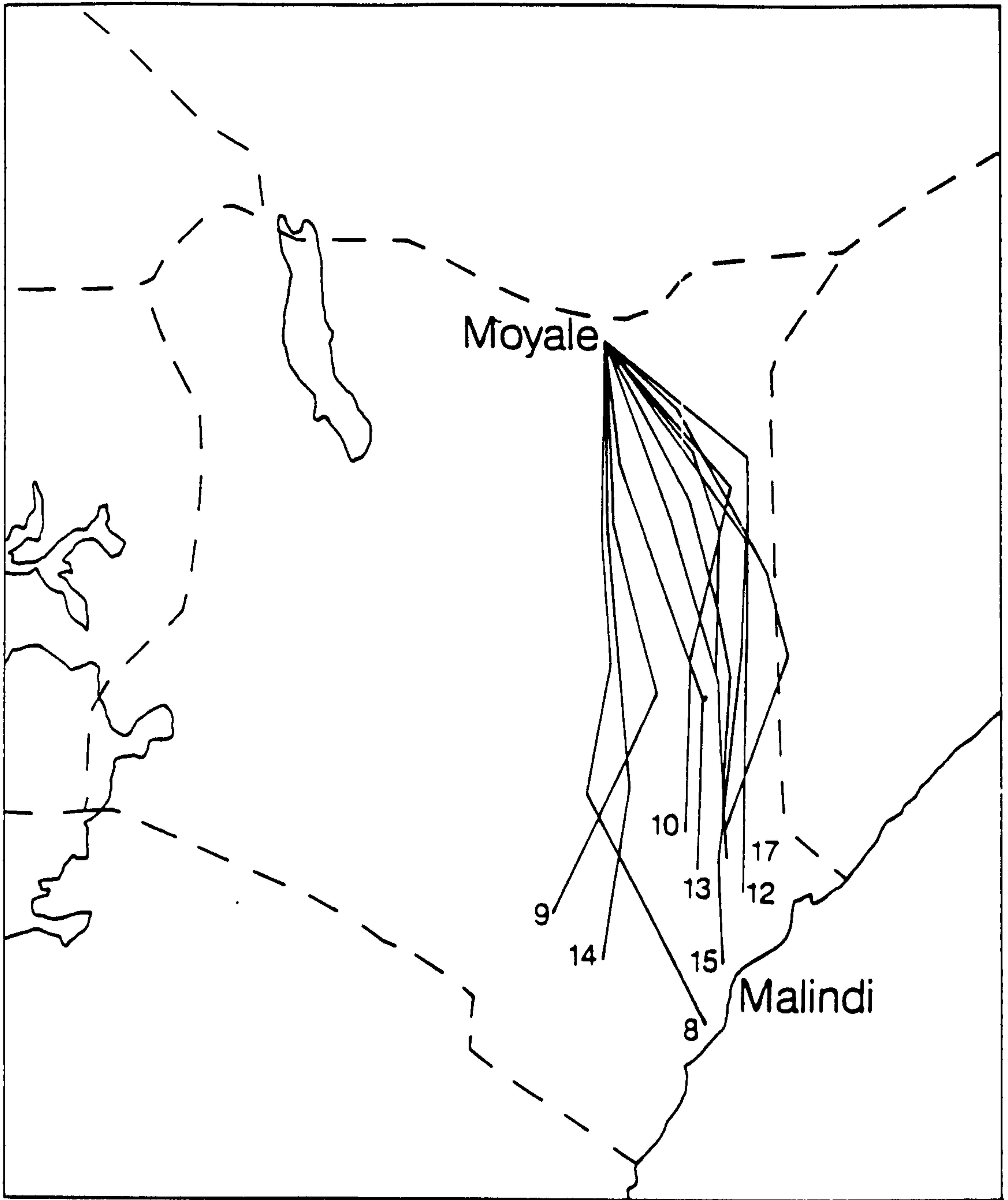


Figure 14. Backtracks from outbreaks at Moyale and neighbouring areas of Sidamo in southern Ethiopia with moth arrival 10-20 May 1984.

Secondary outbreaks derived from south-east Tanzania primary outbreaks and from Malawi

Forward tracks for moth emergence from early primary outbreaks in south-east Tanzania went towards the west or south-west. Secondary outbreaks were only reported in southern Tanzania in three seasons (1976-77, 1981-82, 1983-84) with a single generation followed by a gap from February to the end of October, when there were no outbreaks. Forward trajectories gave no evidence for moth migration northwards from south-east Tanzania. Outbreaks were, therefore, not 'critical' for subsequent outbreaks in Tanzania.

In one season (1976-77), backtracks indicated that widespread first outbreaks in Nachingwea and Tunduru districts in January were derived from earlier outbreaks reported in Malawi in December (Figure 42), with eastward migration made possible by an unusual spell of surface westerly winds in southern Tanzania from 31 December to 3 January (Fig 12).

Seasons with very few or no secondary outbreaks

There were two seasons with no secondary outbreaks (1972-73 and 1977-78). These had single primary outbreaks near Kisumu in western Kenya (in December 1972 and February 1978) but no early outbreaks in the main primary outbreak areas. Both seasons had well above average October to December rainfall, and rain fell on most days in November 1977 in east-central and south-east Kenya. In 1982-83, there were only one small primary outbreak in south-east Kenya in October and two small primary outbreaks in east-central Tanzania in December, followed by four small, low-density secondaries there in January. The lack of further outbreaks in this season was almost certainly due to the exceptionally heavy rains which started very early

(late September to early October) and persisted into December. Voi had four times the average October rainfall and Morogoro had more than twice the average December rainfall, with rain falling on most days in these months. Persistent wet weather has been found to be associated with high levels of infection of armyworm by nuclear polyhedris virus, causing high larval mortality (Persson 1981).

In May 1973, after no outbreaks in Tanzania all season, outbreaks suddenly appeared in east-central and north-east Tanzania. Winds were southerly suggesting migration from unreported sources in the south; or there may have been a late, unusual build up from local low-density populations, indicated by persistent moth catches in light traps from December to February.

(v) Critical outbreaks

Matrices of source/destination interactions are shown in Tables 5,6. 'Critical' outbreaks are most likely to occur in $2 \times 2^\circ$ squares which were frequent sources for other outbreaks in the 16 years analysed. In the period October to December, the most frequent sources, underlined in the rowsum, corresponded closely to the areas of most frequent primary outbreaks, as shown in the map of percentage frequency (Fig 15). The main difference from the frequency of primary outbreaks (Fig 8) is that the percentage frequency for squares covering north-east Tanzania-Taveta ($2-4^\circ\text{S } 36-38^\circ\text{E}$ and $4-6^\circ\text{S } 36-38^\circ\text{E}$) is as high as that for east-central Tanzania ($6-8^\circ\text{S}, 34-36^\circ\text{E}$ and $6-8^\circ\text{E } 36-38^\circ\text{E}$). Destinations were more scattered than sources, as might be expected if moths tended to disperse downwind, with eight squares having more than ten occurrences compared with five for sources. Migration of less than about 200km was indicated where sources and destinations were in the same square. Longer distance

Table 5. The frequencies of occurrence of migrations from sources (grid squares of 2 x 2 degrees) to destinations during October-December 1972-1987. The numbers on the axes refer to the southern and northern bounds of the square and the longitude (degrees E) of its western edge.

Table 6. The frequencies of occurrence of migrations from sources (grid squares of 2 x 2 degrees) to destinations during January-June 1973-1988. The numbers on the axes refer to the southern and northern bounds of the square and the longitude (degrees E) of its western edge.

SOURCE JANUARY TO JUNE

DESTINATION	4-6N		2-4N		0-2N		0-25		2-45		4-65		6-85		8-105		TOTAL																						
	32	34	36	38	40	32	34	36	38	40	32	34	36	38	40	32		34	36	38	40																		
4-6N	1																				0																		
2-4N					1																0																		
0-2N																					0																		
0-25																					0																		
4-65																					0																		
6-85																					0																		
8-105																					0																		
TOTAL	0	0	1	0	0	3	0	1	0	0	4	26	10	1	0	1	23	39	5	1	4	9	34	11	5	0	9	0	6	0	2	4	0	0	0	0	0	0	201

DESTINATION

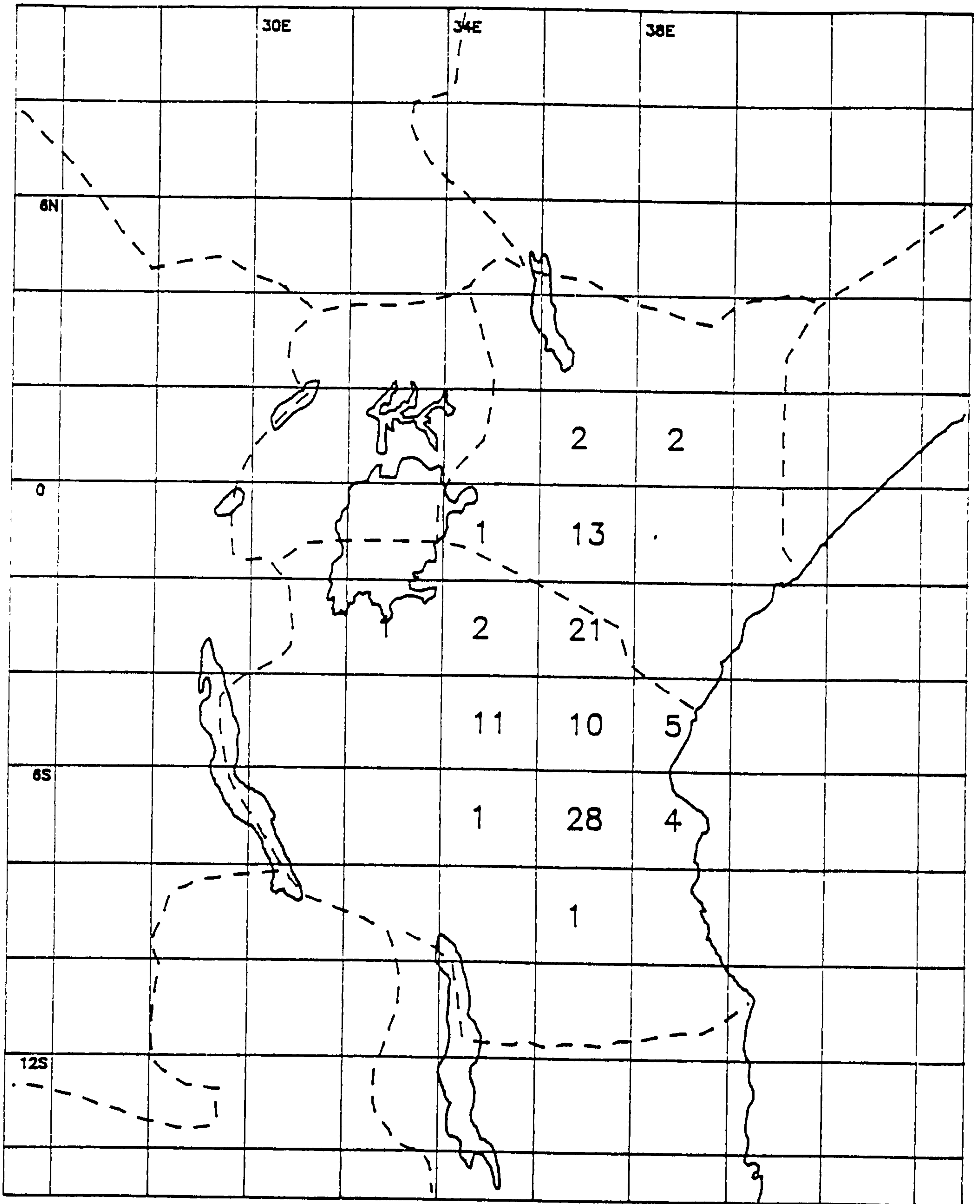


Figure 15. Frequency (as a percentage) that two degree squares had outbreaks which were sources of further armyworm outbreaks, October-December.

migration was indicated to destinations in western Kenya ($0-2^{\circ}\text{S}$, $34-36^{\circ}\text{E}$), north-western Tanzania ($2-4^{\circ}\text{S}$, $32-34^{\circ}\text{E}$ and $2-4^{\circ}\text{S}$ $34-36^{\circ}\text{E}$) and southern Uganda ($0-2^{\circ}\text{N}$, $32-34^{\circ}\text{E}$).

In January to June, east-central Kenya and north-east Tanzania were the main source areas and central Tanzania was no longer an important source (Table 6, Fig 16). Western Kenya ($2^{\circ}\text{N}-2^{\circ}\text{S}$, $34-36^{\circ}\text{E}$) had become an important source area. Migrations of less than 200km were frequent judging by the many sources and destinations in the same squares, especially in western Kenya. Northern Uganda, northern Kenya and southern Ethiopia, covering the area $2-6^{\circ}\text{N}$, $32-40^{\circ}\text{E}$, appeared as new destinations following long-distance migrations from sources to the south or south-east. Migration will be considered in more detail in the next chapter.

Squares where 'critical' outbreaks are frequent are those where strategic control is likely to be successful. In October to December, these are in the primary outbreak areas. From January to June, strategic control of outbreaks in east-central Tanzania no longer seems justified. 'Critical' outbreaks are most likely in northern Tanzania and central and western Kenya. The high frequency of destinations in the same squares, which all contain important cereal-growing areas, suggests that control measures are justified against these outbreaks on strategic and tactical grounds.

The squares in which 'critical' outbreaks are likely to occur cover very large areas and it is unlikely that all such outbreaks could be controlled in a strategic control exercise. Nevertheless, these results suggest areas within Kenya and Tanzania where control resources should be concentrated in the early and late parts of the armyworm season.

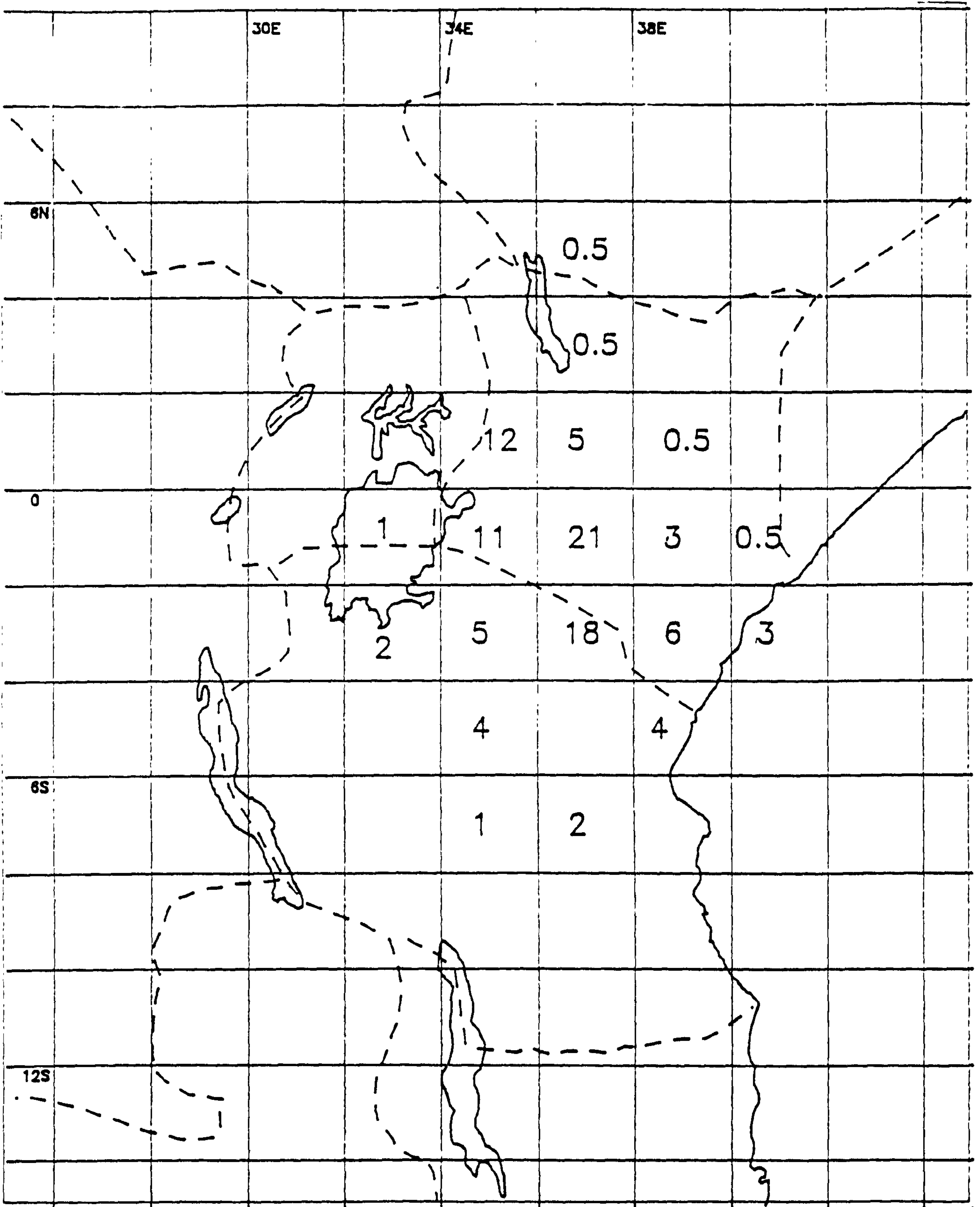


Figure 16. Frequency (as a percentage) that two degree squares had outbreaks which were sources of further armyworm outbreaks, January-June.

The decision to carry out strategic control should be based on assessment of the economic cost of crop damage likely to arise if the outbreaks are not controlled. Frequencies of secondary outbreaks following source outbreaks in particular areas, together with analyses of cereal production figures and likely crop loss in the destination area, are being used in such an assessment (Cheke & Tucker 1995).

(v) Low-density populations

The results indicated that moths initiating early primary outbreaks came from low-density armyworm populations near the coasts of Kenya and Tanzania, where grass may remain green during the dry season.

Strategic control of 'critical' outbreaks, aimed at preventing outbreaks in future generations, would be unsuccessful if large, low-density sources persisted during the season. The occasional occurrence of large, apparently primary outbreaks on the coast between November and May, suggests that low-density populations can persist there during the armyworm season, but the proportion of the population that remains at low density is not known.

Gatehouse (1986, 1987) suggested that such populations would probably not remain at low density if they migrated inland, because they would encounter a generally dry, patchy habitat where successful breeding would depend on being concentrated by rainstorms, when outbreaks would form. Occasional primary outbreaks in wetter, western areas of Tanzania and Kenya indicate that low-density populations may persist there during widespread rains, which are generally unsuitable for primary outbreak formation. Low-density armyworm populations also sometimes persist in south-eastern Ethiopia, judging by

trap catches, and these may initiate primary outbreaks in the same area.

Armyworm remained at low density in seasons when early rains were heavy and widespread. In moderate or severe seasons, few moths were caught in light and pheromone trap between outbreak generations, supporting the hypothesis that, during the armyworm season, most armyworm live in outbreaks, not in low density populations (Rose et al 1987).

After the beginning of the season, outbreaks were often backtracked to earlier ones, again supporting the hypothesis that most of the armyworm population occurs in outbreaks. This provides justification for using forward tracks from outbreak moth emergence, to areas where wind convergence may result in further outbreaks, as a method of forecasting armyworm occurrence.

CHAPTER 5. FREQUENCIES OF PARTICULAR MIGRATIONS BETWEEN
SPODOPTERA EXEMPTA OUTBREAKS AND DISTANCES
COVERED, BASED ON TRAJECTORIES.

(a) Introduction

As discussed in Chapter 1, African armyworm moths are obligate migrants, which emigrate from their emergence site, disperse, oviposit and die (Johnson's Class 1 migration - Johnson 1969). The distance over which the moths migrate depends on the duration of flight (how many nights and how long on each night), on the direction of flight in relation to the wind direction, and on the persistence and speed of the wind.

The migratory potential of *Spodoptera exempta* moths has been studied in the laboratory (Parker & Gatehouse 1985a,b, Woodrow et al 1987, Wilson & Gatehouse 1993). They found that migration occurs in every generation but that migratory potential is modulated by phase polyphenism. The gregaria phase *Spodoptera exempta* moths generally have a higher flight capacity than the solitaria phase but there is considerable genetically-based variation. As this species migrates pre-reproductively, Wilson & Gatehouse (1993) have used the duration of the pre-reproductive periods of adults reared from different outbreaks as a measure of migratory potential of armyworm moths. They concluded that moths originating from early season outbreaks in regions of low, variable rainfall had a higher migratory potential than those from outbreaks in areas of high, consistent rainfall and those late in the season when suitable habitats are widely distributed.

Brown et al (1969) were the first to study moth migrations from field reports. From maps of outbreak reports they deduced probable migrations between

outbreaks in Ethiopia from April to June 1966. These migrations covered about 700km between generations and were in a general downwind direction. Trajectory analysis of moth migration, based on daily windfield analyses, can provide more precise estimates of both the direction and length of such long-distance migrations, provided migration is downwind. As previously discussed, radar and mark-capture evidence has shown conclusively that migration is predominately downwind and that moths can cover distances of at least 147km in two nights and possibly in one night (Riley et al 1983, Rose et al 1985). Trajectories were calculated by Tucker et al (1982) and Tucker (1984) from increases in light trap catches, and back from first outbreaks of the season, respectively. In the present work, trajectories have been calculated for moth migrations leading to outbreaks and for moth migrations following emergence from outbreaks. Where backtracks indicated that sources were previous outbreaks and where forward tracks indicated that moths gave rise to new outbreaks, these analyses could be used to estimate migration distances between outbreaks.

The analyses of changes in distribution of African armyworm outbreaks during 16 armyworm seasons were used to assess the frequencies of particular migrations, the likely distances flown by moths from different outbreaks and the possibility of return migration from Ethiopia to Kenya.

(b) Methods

Seasonal maps of African armyworm outbreak distribution plotted on a degree square grid were used to estimate straight-line migration distances between source and destination outbreaks, as derived from trajectory analyses, for each 'moth arrival' month. Although trajectories were often not straight lines, the overall

displacement was considered more important from an epidemiological or ecological point of view than the actual distance flown by individual moths.

Since one degree is approximately 100km, distances were measured assuming that outbreaks in adjacent one degree squares were 100km apart and outbreaks in the next corner square were 150km apart. Migrations between more distant squares were similarly measured as distances between the centres of the squares. Where subsequent outbreaks occurred in the same degree square, the migration distance were assumed to be 50km, although many were likely to be shorter than that. Migrations were, therefore, effectively measured in 50km classes. Frequencies of migration distances were then tabulated and analysed by 100km classes for 3-monthly periods, October-December, January-March and April-June, corresponding to early, mid and late armyworm season. Migrations north of 10°N were not considered due to lack of data.

The matrices of interactions between 2 * 2 degree squares with source outbreaks and those with destination outbreaks, used in identifying 'critical' outbreaks (Tables 5,6), were also used to assess the frequencies of migrations between particular 2 * 2 degree squares in the periods October to December and January to June. As discussed in Chapter 4, there were too few interactions between individual one degree squares for the source/destination frequency analysis. Migration direction, distance and frequency were summarized for the main source squares using frequency rose maps.

The degree square data could not be used to assess the role of particular wind regimes in moth migrations. For this, individual trajectory analyses, and the windfield analyses on which they were based, were used to assess

the frequencies of occurrence of long-distance moth migrations, defined as migration over distances of more than 100km, in relation to particular wind regimes. The possibility of long-distance moth migrations not identified from the current data, such as southward return migration from Ethiopia, was then assessed in relation to possible unreported armyworm outbreaks and both usual and unusual wind regimes.

(c) Results (Tables 5,6; Figs 17-23)

(i) Migration distances.

The frequency distribution of migration distances, taken as a percentage for comparison between periods (Figure 17), indicated an inverse relationship between distance and frequency, with large numbers of relatively short migrations of less than 100km and a few very long ones. The highest proportion of both short and very long migrations occurred in April-June when 62% of measured migrations were of less than 100km (taken as 50km for the purpose of calculating the mean) and 11% were of 500km or more. For October-December, 32% of migrations were less than 100km and 4% were 500km or more; for January-March the corresponding percentages were 41% and 8%. The percentage frequencies of moth displacements of between 100 and 400km, which are the sort of distances indicated by the mark-capture experiment (Rose et al 1985) and which might be considered more usual long-distance migrations, therefore varied from 65% for October-December to 53% for January-March and only 22% for April-June. October-December and January-March periods showed some differences in distribution of migration distances, with more migrations of 100-200km and 700-800km in the earlier period but more of 300-600km in the latter period. The mean migration distances were not significantly different between periods and were 165km,

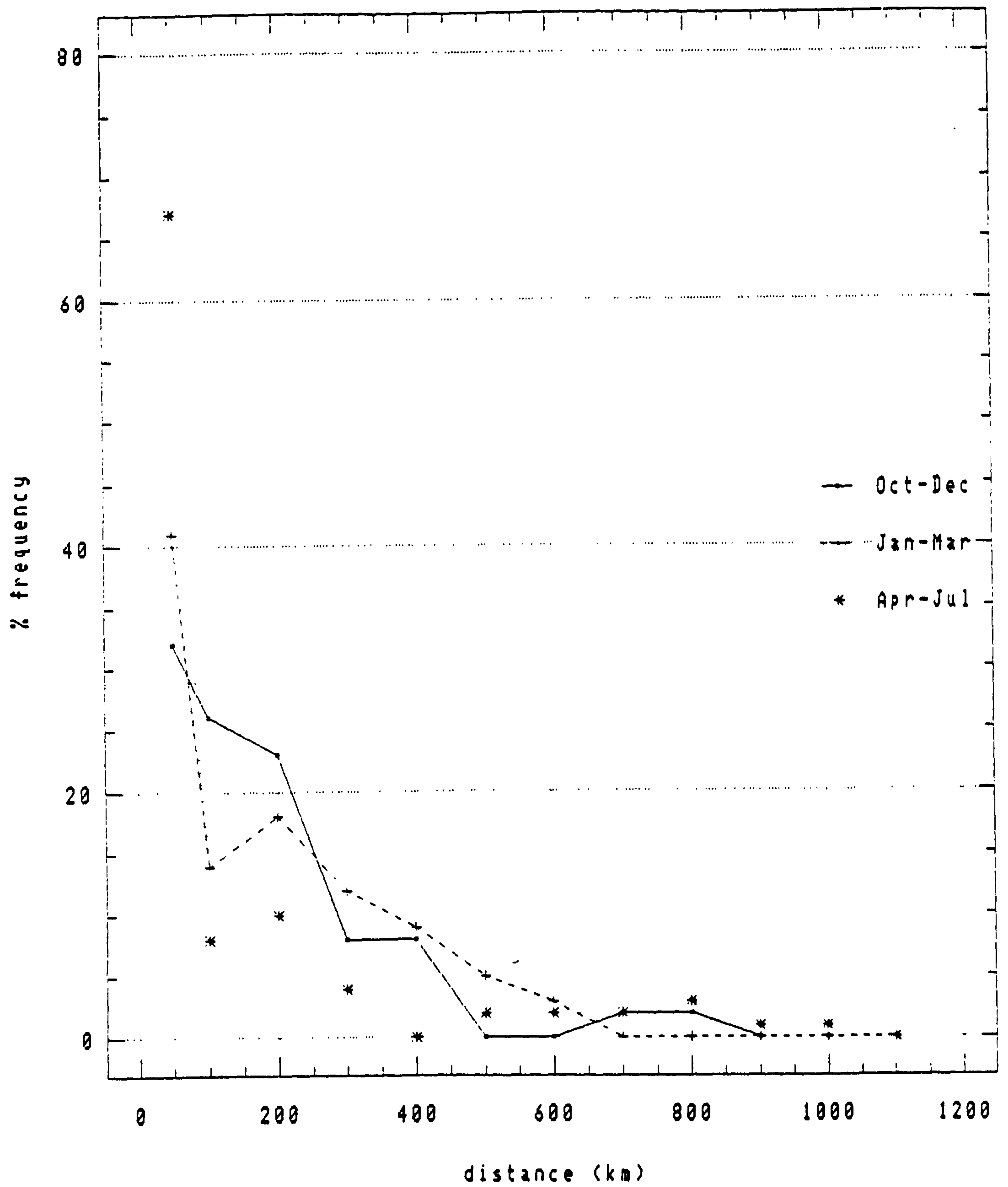


Figure 17. Percentage frequency of distances of armyworm moth migrations between outbreaks for early, mid and late armyworm seasons.

179km and 158km for October-December, January-March and April-June respectively. The median distances for the classified data were 100km for October-December and January-March and 50km for April-June.

(ii) Migration directions

A general idea of the direction of migrations can be obtained from the 2 * 2 degree matrix of source and destination armyworm outbreaks for the two periods October-December and January-June (Tables 5,6). For January-June all migrations are in the top right-hand part of the matrix indicating that (for migrations of >100km) sources were always south of destinations. This would be expected for April-June when winds are southerly or south-easterly but is more surprising for January to March when north-easterly winds are present over much of eastern Africa. It is explained by the frequency of outbreaks in northern Tanzania and south-western Kenya where south-easterly winds often occur. In October to December there were a few southward movements but, again most movements were towards the west or north-west. Differences between eastward and westward movements are not clear from the matrix but frequency rose maps for the most frequent source squares (Figs 18-25) show that, for October to December, only 3 out of 83 migrations between squares were towards the east and, for January to July, 3 out of 37, all to the north-east. The most frequent migration directions for these particular source squares were towards the northwest and west for October to December and towards the north and northwest for January to July. Differences are apparent between source squares. In October to December all migrations from 0-2°S, 36-38°E (east-central Kenya) were to the west or southwest, whereas from Morogoro, Arusha and Singida squares in Tanzania many migrations were to the northwest. In January to June very long distance northward migrations

(600-1000 km) occurred from southeast Kenya and northeast Tanzania towards Ethiopia but not from east-central or western Kenya.

Table 7 shows the winds associated with long-distance downwind migrations, as deduced from individual trajectory analyses, and the months and seasons in which they occurred.

From November to March, long-distance migrations occurred on the dominant easterly winds. These were easterly to north-easterly in Kenya but easterly to south-easterly in Tanzania. Migrations out of the primary outbreak areas in east-central Tanzania, north-east Tanzania and east-central Kenya, towards the west or north-west, were particularly significant when they were followed by further westerly or north-westerly movement in the next generation, leading to outbreaks in cultivated areas near Lake Victoria in north-west Tanzania, western Kenya and southern Uganda.

Migrations in east-central and central Kenya were often relatively short-distance (<100km) and the frequency of long-distance migration was lower than for other primary outbreak areas. Long-distance migrations into east-central Kenya were sometimes caused by windfield disturbances (e.g. in 1987-88).

In April and May, the dominant winds shift to south-easterly or southerly and long distance armyworm migration often occurs towards the north. In eight seasons, northward migration from northern Tanzania, east-central Kenya or the Kenya coast covered from 800-1000km and led to outbreaks in southern Ethiopia. The onset of the low-level southerly jet stream (see p 33) made these moth migrations possible at heights of several hundred metres above the ground.

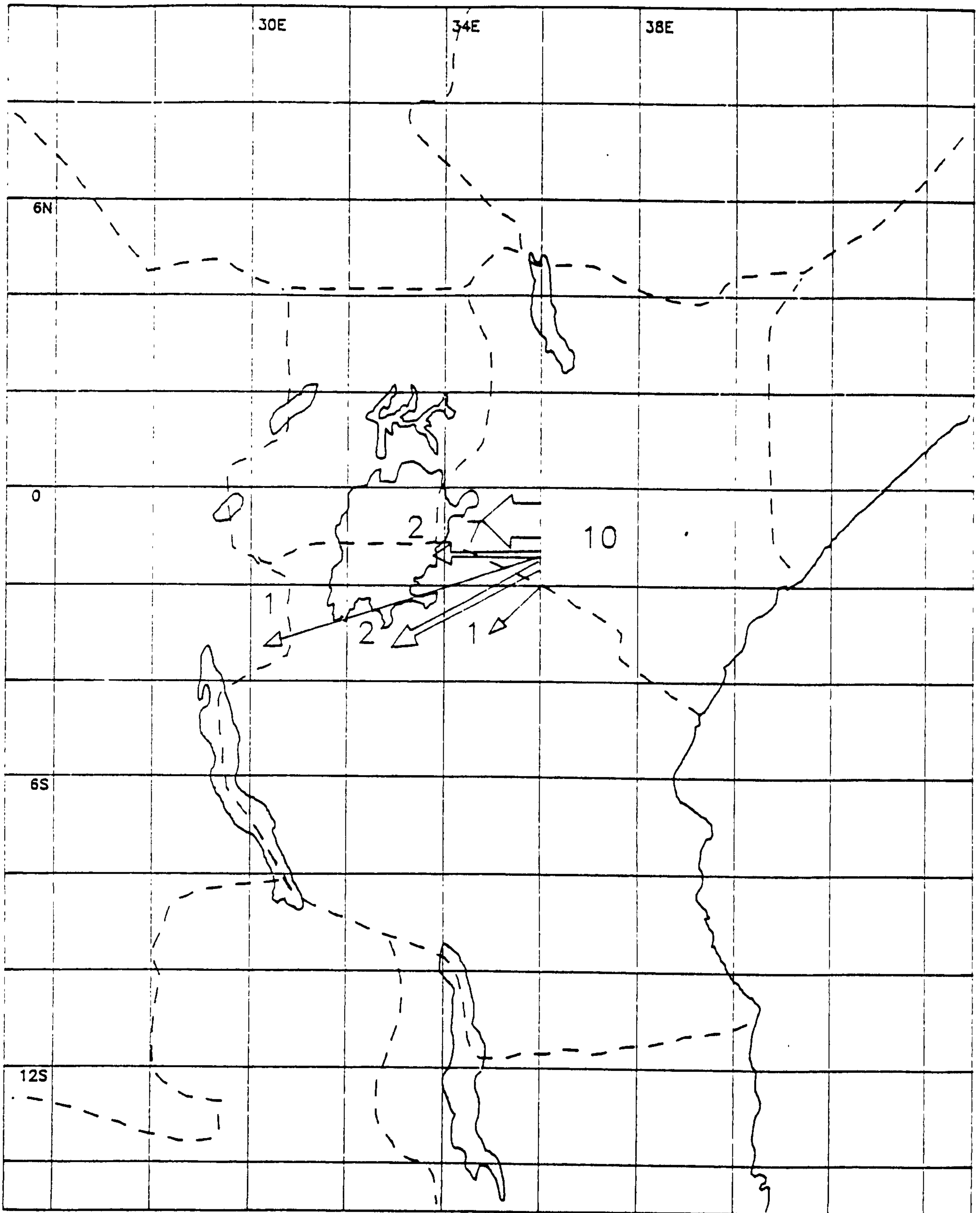


Figure 18. Frequency of migrations from source outbreaks in the square 0-2S, 36-38E, October-December.

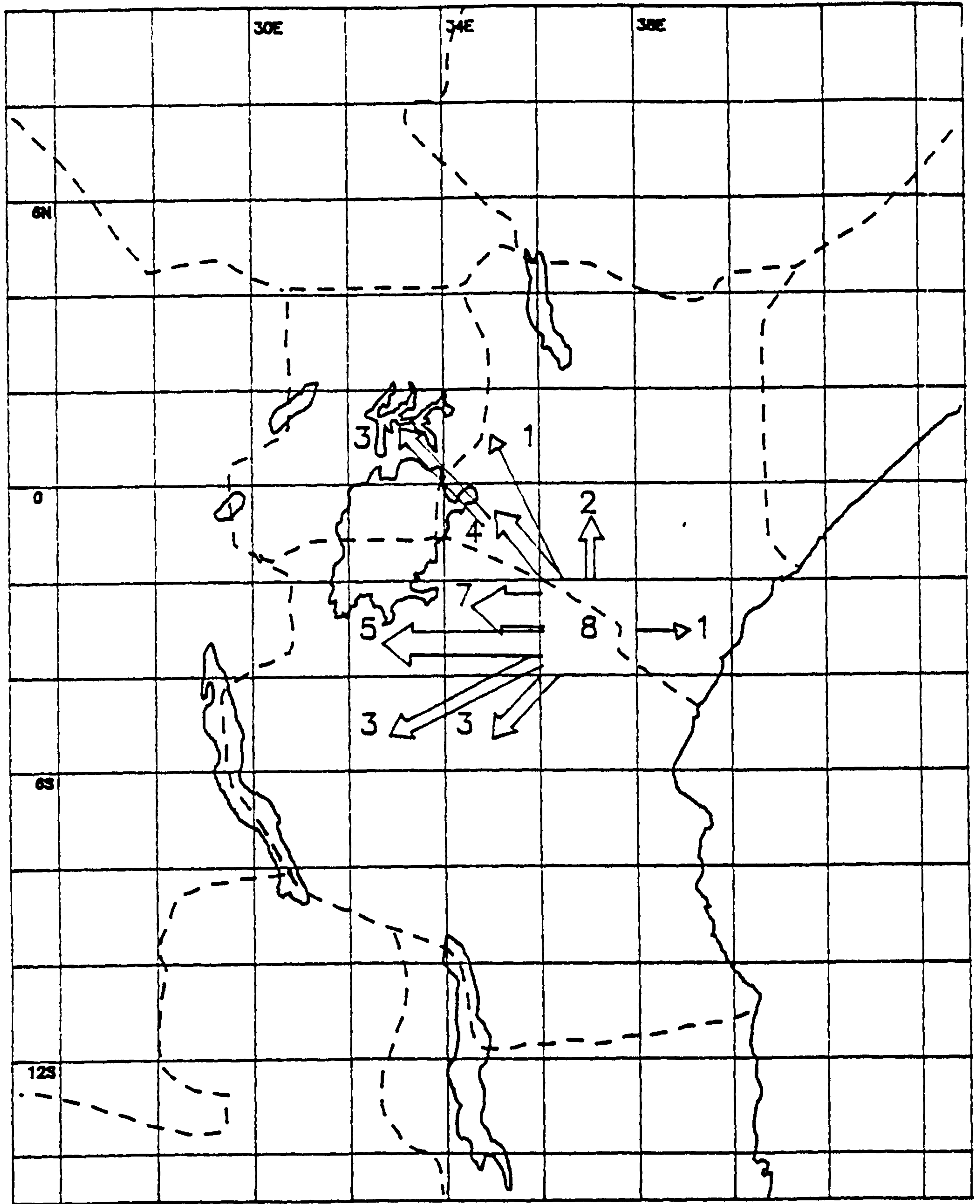


Figure 19. Frequency of migrations from source outbreaks in the square 2-4S, 36-38E, October-December.

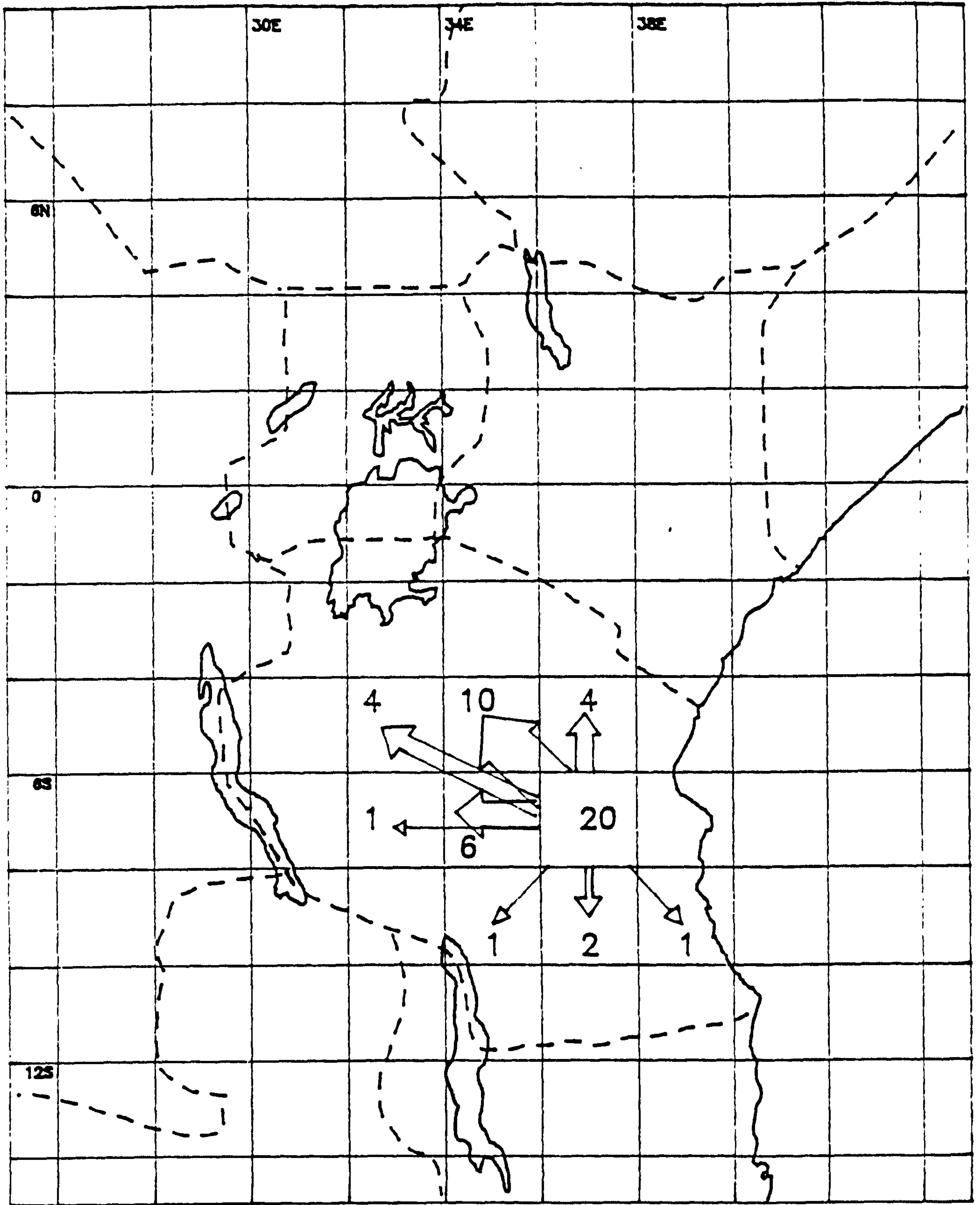


Figure 20. Frequency of migrations from source outbreaks in the square 6-8S, 36-38E, October-December.

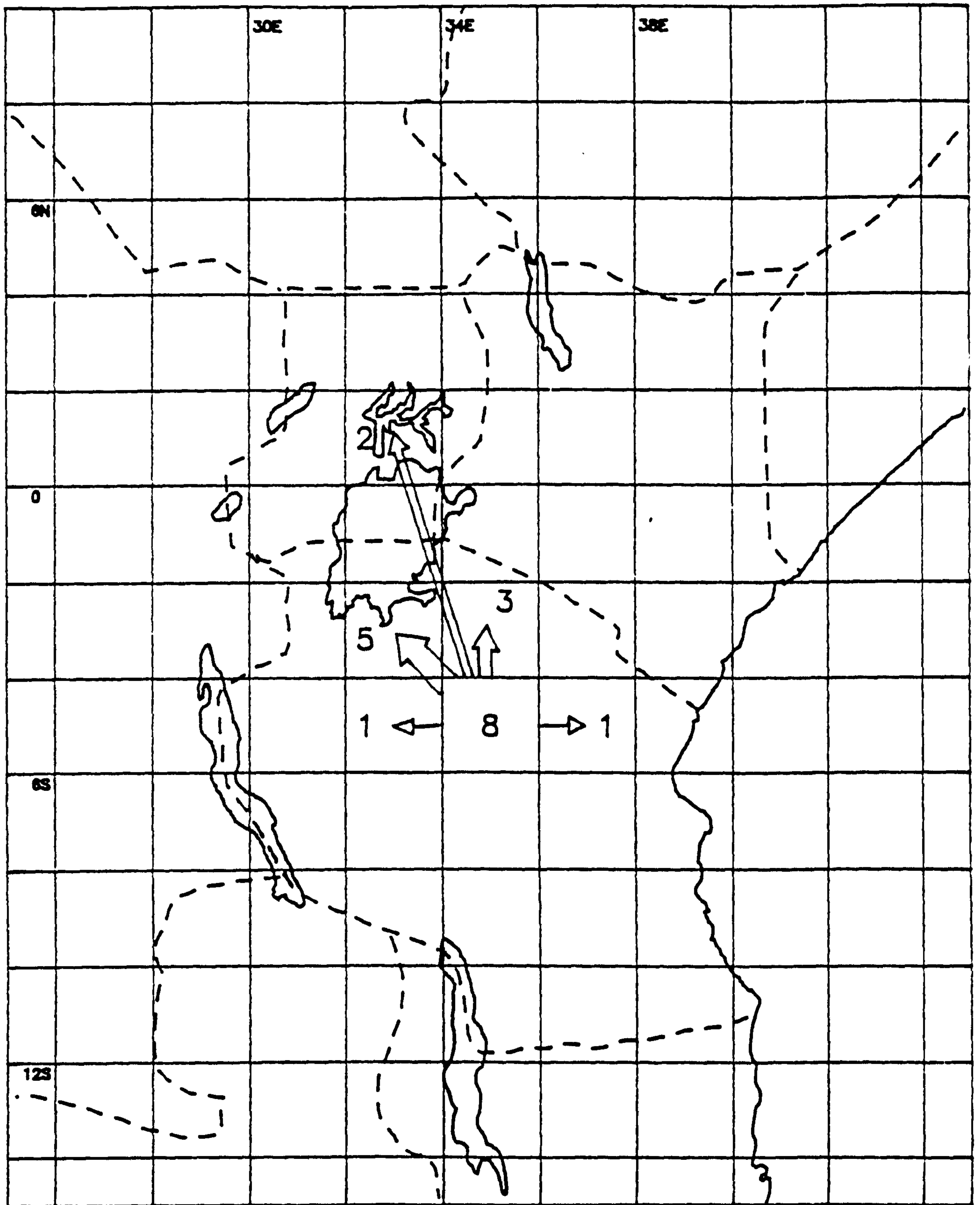


Figure 21. Frequency of migrations from source outbreaks in the square 4-6S, 34-36E, October-December.

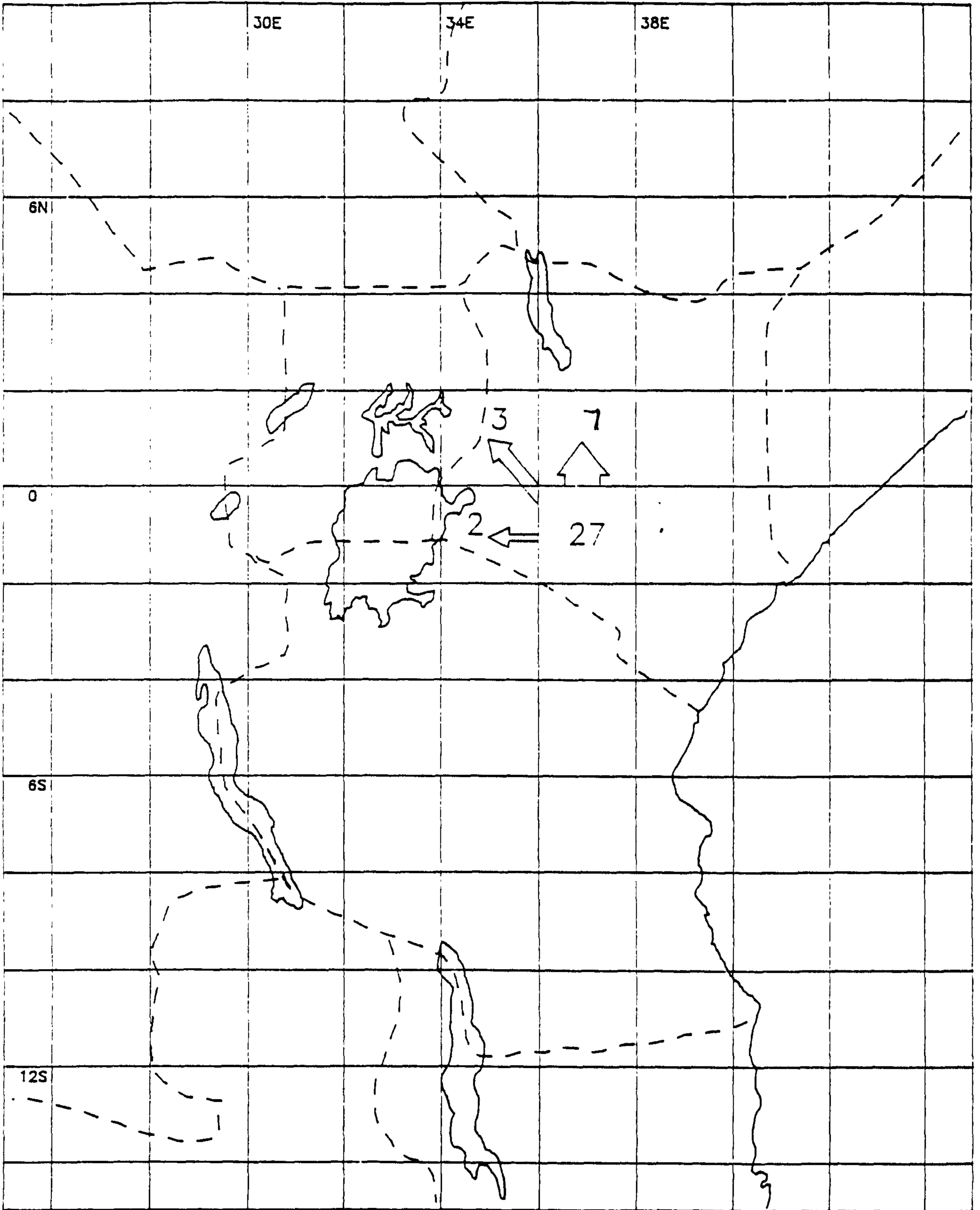


Figure 22. Frequency of migrations from source outbreaks in the square 0-2S, 36-38E, January-June.

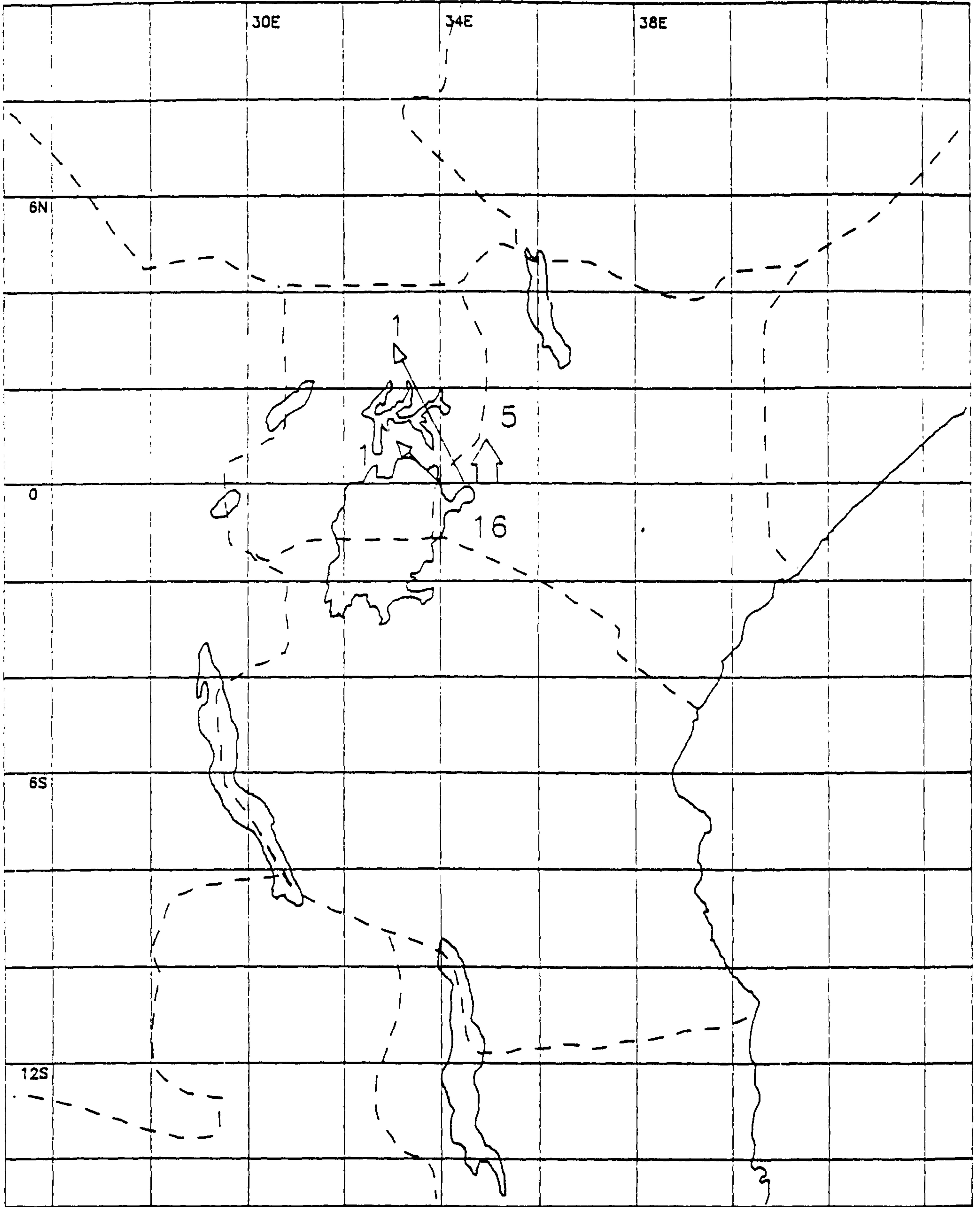


Figure 23. Frequency of migrations from source outbreaks in the square 0-2S, 34-36E, January-June.

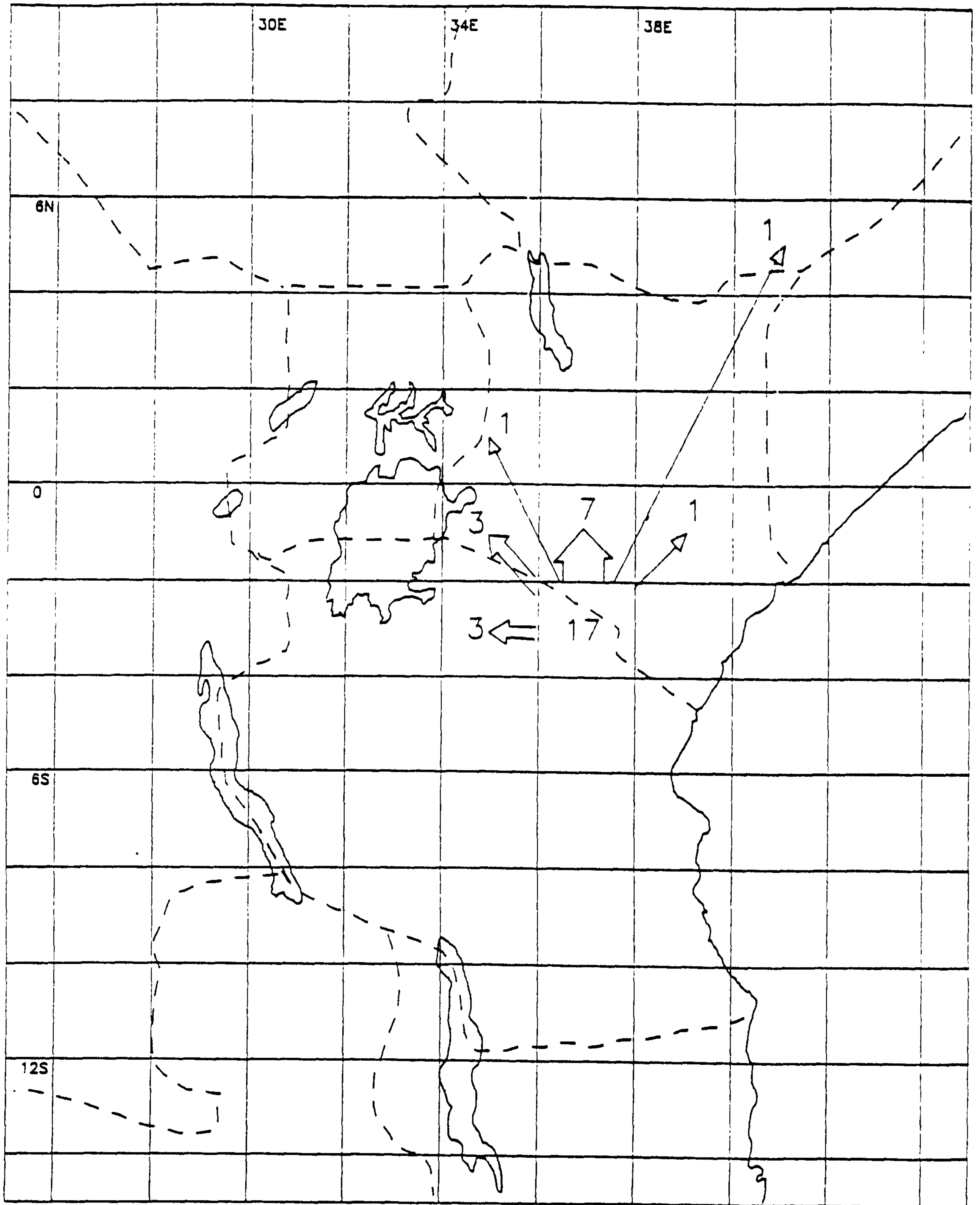


Figure 24. Frequency of migrations from source outbreaks in square 2-4S, 36-38E, January-June.

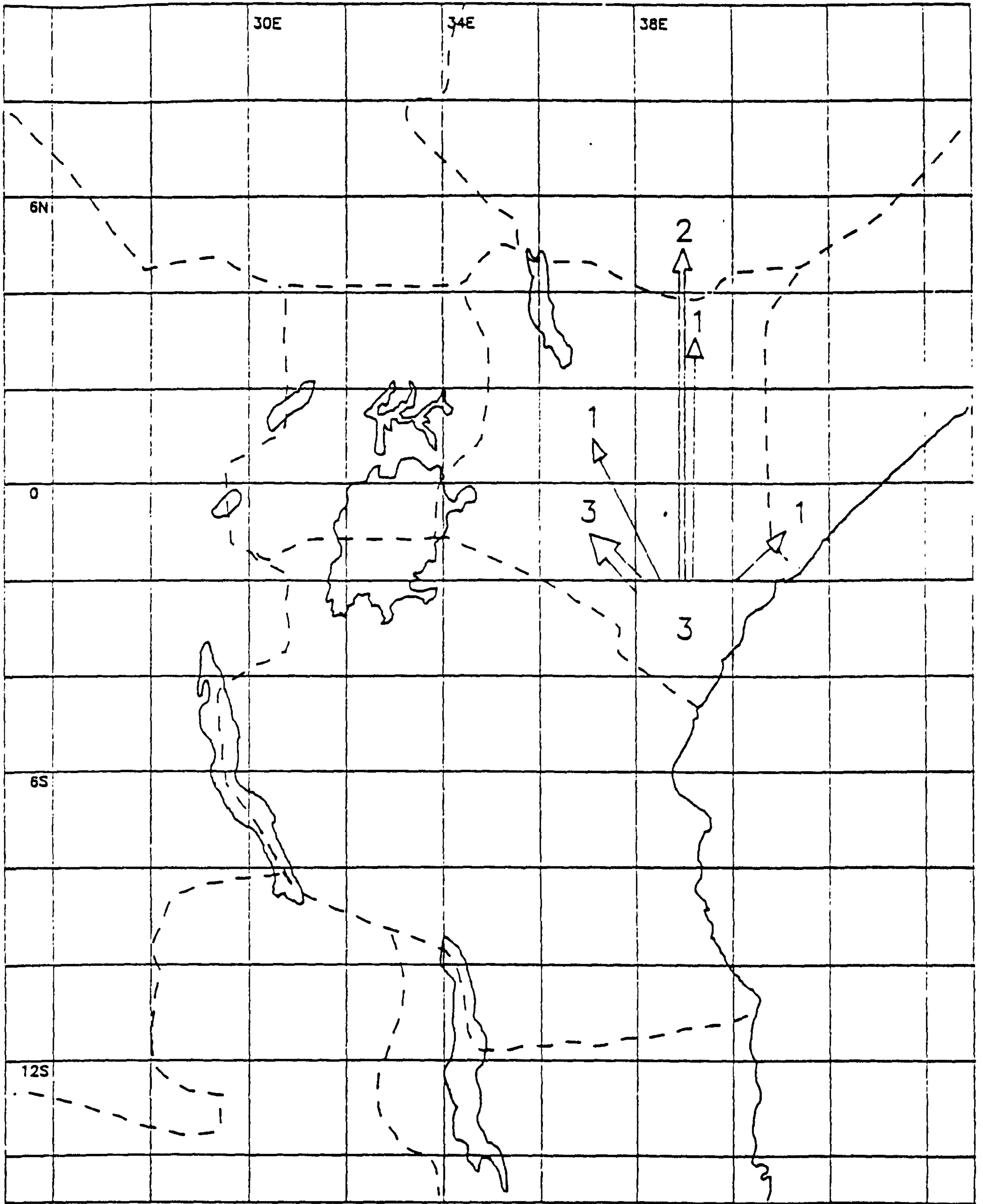


Figure 25. Frequency of migrations from source outbreaks in square 2-4S, 38-40E, January-June.

Table 7. Long distance armyworm moth migrations, deduced from trajectory analyses, and large-scale winds associated with them.

Months	Migration	Approximate distance km	Associated Winds	Seasons
Nov - Dec	S Somalia to E-Central Kenya	600	Strong easterlies - north-easterlies	1978-79 1980-81 1985-86
"	E-Central Kenya to NE Tanzania	150	Temporary northerlies	1976-77
"	E-Central Kenya to Burundi	170	Strong north-easterlies	1984-85
Nov - Feb	E-Central Kenya to Central Kenya	150	Easterlies - north easterlies	1978-79 1979-80 1980-81 1984-85
"	Central Kenya to W Kenya/ N Tanzania	300	Easterlies	1976-77 1979-80 1980-81 1984-85 1985-86 1986-87
"	E-Central Tanzania to Central Tanzania	450	Easterlies to southeasterlies	1973-74 1975-76 1976-77 1981-82 1984-85 1986-87 1987-88
Jan	Malawi to SE Tanzania	600	Temporary westerlies	1976-77
Jan - Mar	Central Tanzania to N Tanzania/ Uganda	650	Southeasterlies	1973-74 1975-76 1976-77 1979-80 1981-82 1986-87 1987-88
Jan - Mar	NE Tanzania to N Tanzania/ W Kenya	450	Southeasterlies	1975-76 1976-77 1978-79 1979-80 1981-82 1986-87 1987-88
Mar - May	NE Tanzania/SE Kenya to E- Central Kenya	250	Temporary southerlies in March Southerlies in April-May	1981-82 1987-88 1973-74 1974-75
Apr - May	E-Central Kenya/NE Tanzania to S Ethiopia	800	Strong southerlies	1973-74 1974-75 1975-76 1976-77 1979-80 1987-88
"	S Kenya coast to W Kenya coast/ S Somalia	450	Southerlies to south- westerlies	1981-82 1987-88
"	Kenya coast to W Kenya/S Ethiopia	950	Strong southerlies	1976-77 1981-82 1983-84 1987-88

(d) Discussion

(i) Migration distances.

Analyses of the pre-reproductive periods of *Spodoptera exempta* moths sampled from outbreaks at various times and locations indicated that migratory potential decreased later in the season and in areas where rains are more persistent (Wilson & Gatehouse 1993). The present results show a decrease in median migration distance late in the season, with an increase in the proportion of short migrations but also with a small proportion of very long migrations. The very long migrations were all from eastern Kenya or adjacent north-eastern Tanzania towards Ethiopia. Thus the capacity for long duration migratory flights was still present, at least in moths derived from outbreaks in these areas.

It would be useful to clarify exactly what the present results show and how they compare with results from laboratory studies. The distances measured in the present work are a function of the number of nights the moths were flying and the windspeed. The number of nights was constrained between 1 and 5 (based on previous laboratory work) so there was no independent assessment of flight capacity of the moths. Some estimate of the number of nights actually flown could have been obtained if trajectories regularly intercepted source or destination outbreak locations in less than 5 nights. However, as trajectories were calculated for moth 'arrival' or emergence periods of up to 11 days, there was a considerable scatter of trajectories and, as has previously been discussed, general indications of likely migrations rather than precise routes and durations were obtained. The results were, therefore, not considered

precise enough for estimations of numbers of nights flown between outbreaks to be made.

Variations in wind speed through the season and by location were very important in determining the length of trajectories and therefore of estimated moth migrations. High wind speeds were associated with undisturbed easterly flow early in the season and with monsoon southerlies in eastern Kenya from April to July. Low wind speeds were associated with large-scale convergence zones, such as the Zaire Air boundary in the west of Kenya and Tanzania, and very variable winds (often light but sometimes strong locally) with widespread rainstorms. Thus there was generally a tendency for estimated migration distances to decrease westwards and with increasing rainstorm frequency as the rainy seasons developed. In April-June this resulted in a general decrease in migration distance except in the strong southerly winds.

The present study, therefore, looked mainly at variation in migration potential based on the effectiveness of the wind in transporting migrating moths rather the potential of the moths themselves (as considered by Wilson & Gatehouse, 1993). The two studies would be linked, however, if the flight capacity of the moths had evolved to maximise the potentiality of downwind migration. It would then be expected that migratory potential would be high for moths emerging in eastern parts of Kenya and Tanzania, and in the dry season or at the beginning of the rainy seasons, when rains are scattered, and low in western parts and in the mid and late rainy seasons. This fits well with the results of Wilson & Gatehouse (1993), except that high migratory potential was maintained in many moths emerging in eastern Kenya in the long rains, judging by the evidence of long distance migrations to Ethiopia on strong southerly winds (e.g. p 71).

(ii) Migration directions

In spite of the apparent seasonal shift of *Spodoptera exempta* outbreak populations from Kenya and Tanzania from November to May, to Ethiopia from April to August, the results give no evidence for a return migration from Ethiopia to Kenya at the beginning of the season in Kenya and Tanzania. As critical primary outbreaks in Kenya frequently had moth arrival dates in October, when winds in Kenya were south-easterly, southward migration from Ethiopia was not possible. Even when winds shifted to easterly or north-easterly, backtracks from primary outbreaks came from eastern Tanzania, eastern Kenya or southern Somalia with no known sources north of 2°N.

This does not rule out the possibility of very occasional southward migrations. Outbreaks in southern Ethiopia in September 1978 (Fig 44) show that outbreaks do occasionally occur there immediately preceding the usual start of the season in Kenya. If outbreaks were also present further east (in the Ogaden or north-eastern Somalia) and/or if a weather disturbance (eg. an Arabian Sea tropical cyclone) led to northerly rather than north-easterly winds over northern Kenya, then southward migration to Kenya would be possible. Such occurrences must be rare and did not occur in the period of study. They would, therefore, not be significant in the seasonal population dynamics of *Spodoptera exempta* but might provide a mechanism for occasional return gene flow from north to south.

An alternative hypothesis that the moths fly in a southward compass direction, rather than downwind, has no support from previous research on *S. exempta*. The present results support previous work by Rose (1979), Rose et al (1987) and Tucker (1984a).

CHAPTER 6. COMPARISON BETWEEN ARMYWORM SEASONS

(a) Introduction

The summaries in the Appendix demonstrate that there is considerable seasonal variation in the severity and development of African armyworm outbreaks in eastern Africa. Previous work has identified a number of environmental and population variables that may be important factors contributing to this variation.

Hattingh (1941) and Brown (1962) considered that, in years when seasonal rains were delayed, young, tender grass often appears at the same time as armyworm hatching, providing favourable conditions for early instars. In South Africa, *Spodoptera exempta* development becomes possible as temperatures rise at the beginning of the summer and the timing may be determined by temperature rather than rainfall. In eastern Africa, however, low temperatures are not a limiting factor in primary outbreak areas so it might be expected that, when rains are late, *Spodoptera exempta* development would be correspondingly late. Janssen & Rose (1990, 1991) and Janssen (1993) found that the nitrogen content of host grasses increased when rainfall followed prolonged drought. Janssen (1993) found that in the period 1988-1991 the occurrence of armyworm outbreaks in the first two months after the start of the short rains in Kitui district, Kenya was associated with increased nitrogen content of food plants following dry weather in the preceding twelve months. Outbreaks occurred during the short rains in 1988 and 1991 (following dry years) but not in 1989 or 1990 (following wet years).

Robinson (1991) used NOAA satellite data, processed to give 7.4 km resolution ('global area coverage') images of the normalised difference vegetation index (NDVI), to

monitor increases in green vegetation in east Africa in relation to armyworm outbreak occurrence. He did not find a good correlation between outbreaks and 10-day increases in green vegetation but concluded that this was partly due to the poor resolution of the processed satellite imagery. He considered that better results would be obtained using full resolution 1.1 km ('local area coverage') NOAA imagery. Robinson found that 7.4 km resolution NDVI could be used as a more general monitoring tool because changes in NDVI on a monthly time-scale reflected the general distribution of armyworm outbreaks, especially if combined with surface temperature data to identify areas and times when air temperatures were outside *Spodoptera exempta* development temperature thresholds. The annual NDVI has been found to be significantly inversely correlated with mean annual saturation deficit in Africa and this relationship has been used as a basis for monitoring tsetse fly (*Glossina spp*) habitats because tsetse mortality is positively correlated with saturation deficit in the previous month during the dry season (Rogers 1991, Rogers & Randolph 1991). Similarly, African armyworm survival in the dry season is likely to be positively correlated with NDVI. Davenport & Nicholson (1993) found that monthly changes in NDVI in east Africa were strongly correlated ($R = >0.7$) with rainfall in the current and previous two months in drier areas, with total annual rainfall $<1000\text{mm}$, but were less well correlated in wetter areas. Similarly, correlations between armyworm outbreaks and NDVI are likely to be best in drier areas. Since these areas include at least parts of the primary outbreak areas, NDVI (at 1.1 km resolution) may be useful for identifying broad areas where primary outbreaks are likely to form.

Persson (1981) found, from experiments using outdoor cages to rear *Spodoptera exempta*, a positive relationship between larval mortality and rainfall and a negative one

between larval mortality and sunshine. Most mortality was caused by nuclear polyhedrosis virus and the incidence of virus was greatest during rainy periods. Persson noted that it has been established that the ultra-violet component of sunlight can quickly inactivate nuclear polyhedrosis viruses.

Inverse correlations between early season rainfall and armyworm outbreak severity have been found by several workers. Tucker (1984b), using 21 seasons data, found an inverse association between high total October to December rainfall, for a combination of source and primary outbreak areas in Kenya and Tanzania, and low total numbers of armyworm outbreaks in these countries and *visa versa*. Harvey (unpublished) found significant inverse correlations ($R = -0.63$) between total November and December rainfall in Morogoro and Dodoma regions (east-central Tanzania) and the logarithm (base 10) of the total annual (July-June) *Spodoptera exempta* moth catches at six light traps in Tanzania for 1962-1982. Haggis (in press) has found that, for 1963-72, there was a significant inverse association between numbers of armyworm outbreaks in Kenya in one season and rainfall in southeastern Kenya in the preceding 6-8 months, not just the short rains at the beginning of the season. Considering separate rainy seasons, she found that severe armyworm seasons in Kenya were significantly associated with low rainfall in the previous long rains (April-May), irrespective of short rains rainfall, suggesting that a severe armyworm season might be forecast well in advance. For low armyworm seasons, an association with heavy rainfall was only significant when both long and short rains were included.

Taylor (1986) examined *Spodoptera exempta* catches for five light traps: Muguga (Kenya), Ilonga and Tengeru (Tanzania), and Kawanda and Serere (Uganda). Data for

Muguga were for 10.5 years (January 1963 to June 1973) and for the other traps, 7 years (January 1963 to December 1970). He identified periodicities of high catch at one lunar month, one year and four years. The lunar and annual cycles are well known (Bowden 1973, Odiyo 1987) but the four-year cycle was new. The peak of the annual cycle varied with latitude of the trap, with Tanzania traps peaking before those further north. The four-year cycle, however, corresponded for all traps with peaks in 1966 and 1970, although the amplitude varied between sites. Harvey (unpublished) tested 21 years Tanzania light-trap data for periodicity by autocorrelation for different numbers of years lag. He found that an apparent 5 year cycle was almost, but not quite, significant. However, when the effect of rainfall variation was removed (by subtracting the annual catch predicted from the regression against rainfall from the actual catch), there was no cycle. He concluded that the apparent cycle in armyworm populations (based on moth catches) was caused by a rainfall cycle rather a density-dependent armyworm population cycle.

Independent evidence for some periodicities in short-rains rainfall in eastern Africa has been found, especially for coastal Kenya and southern Somalia (Ropelewski & Halpert 1987, Ogallo 1988, Hutchinson 1992). These were associated with the El Nino/Southern Oscillation Index which affects the Southern Hemisphere ocean/atmosphere system and has a variable cycle of 2-5 years. There were El Nino episodes, with high east Pacific sea-surface temperatures and rainfall, in 1970-72, 1975-77 and 1982-83. These immediately preceded, or coincided with, high October-December rainfall in eastern Africa.

The present chapter compares 16 armyworm seasons in order to identify possible causes of differences, especially

those, such as early season rainfall and the location and timing of 'critical' outbreaks, that might be used to provide seasonal armyworm forecasts.

(b) Data and Methods

The severity of armyworm seasons can be defined and assessed in several ways. The farmer and economist are most interested in the crop loss attributable to armyworm, while the entomologist is more interested in population size of the pest.

Reports of *Spodoptera exempta* usually give estimates of areas covered by outbreaks and these could be used to estimate total area infested in a season. However, these estimates vary greatly in accuracy and reliability, e.g. where a qualitative estimate such as 'whole district infested' has been converted to hectarage; such an estimate is likely to be much too large and would strongly bias the seasonal total.

Alternatively, seasonal severity could be defined by the number of outbreaks. However, this may give a bias towards seasons with many small outbreaks, perhaps of only a few hectares, compared with seasons with fewer, large, damaging outbreaks. Also there are differences between reports that list very many small outbreaks in one district and others that consider this to represent one very large outbreak of varying larval density.

Neither of these measures of severity are satisfactory and it was decided to use 'number of degree squares with outbreaks' as a measure. This gives a conservative estimate that does not vary in accuracy from season to season, even though it measures how widespread outbreaks are, rather than the total population size. The use of 'number of degree squares' partly offset differences in

reporting detail between seasons. For example, 1981-82, 1986-87 and 1987-88 were all severe armyworm seasons in Tanzania with 35, 30 and 31 degree squares infested respectively. However the numbers of outbreaks reported were 90, 210 and 170 respectively, because 1986-87 and 1987-88 were better reported.

Seasonal severity of armyworm outbreaks was measured, for each of the 16 seasons, by the number of degree squares with outbreaks in Kenya and Tanzania, derived from plotted seasonal distribution maps. Ethiopia, Somalia and Uganda were omitted because data were incomplete.

Seasons were also grouped by the country in which there were 'critical' primary outbreaks and the regions in which these outbreaks occurred (Chapter 4), to see if there was any direct relationship between 'critical' outbreaks and seasonal armyworm severity.

An index of October to December rainfall for both Kenya and Tanzania was calculated using data from ten synoptic stations in Kenya and twelve in Tanzania. The October to December total for each station was expressed as a percentage of the mean total, taken from climatological tables (East African Meteorological Department 1975, Kenya Meteorological Department 1984). The mean percentages for these 22 stations were calculated to give an overall rainfall index. Both regression and categorical data analysis methods were used to test whether there was any general association between the indices of 'early season rainfall' and 'overall armyworm severity'. Rainfall indices were also calculated for primary outbreak areas in Tanzania and Kenya separately, using four rainfall stations in Tanzania and three in Kenya, for both short rains and the preceding long rains. These rainfall indices were compared with the number of degree squares with armyworm outbreaks in Tanzania and

Kenya separately, again using regression and categorical data analysis. These analyses were used to further assess the potential for forecasting the severity of armyworm seasons from early-season or previous long-rains rainfall.

Indices of early season rainfall and overall armyworm severity were also plotted against time, to identify any possible trends or cycles. Total seasonal *Spodoptera exempta* moth catches at Muguga light trap, expressed as \log_{10} , were also plotted as an index of seasonal severity, for comparison with the results of Taylor (1986).

(c) Results (Table 8)

Table 8 shows the number of degree squares with outbreaks in Kenya and Tanzania for each season. Taking the totals for Kenya and Tanzania together, seasons could be divided into three distinct classes.

- 'severe' (>33 degree squares with outbreaks),
- 'moderate' (15-25 " " " "),
- 'low' (<6 " " " ").

There were nine 'severe' seasons (indicated by '+' in the last column), four 'moderate' seasons (1974-75, 1975-76, 1978-79 and 1980-81) and three 'low' seasons (1972-73, 1977-78 and 1982-83). On average, severe seasons had 12 degree squares with primary outbreaks and 35 with secondary outbreaks, moderate seasons had 8 with primaries and 16 with secondaries and low seasons had 2 with primaries and 1 with secondaries. This indicates that it is the number of secondary outbreaks that determines the severity of the season. There was no significant difference between numbers of degree squares with primary outbreaks in 'severe' and 'moderate' seasons

Table 8. The severity of armyworm seasons in Kenya and Tanzania (numbers of degree squares infested) in relation to the location and timing of critical primary outbreaks and rainfall.

Season	Critical Primary Outbreaks (Location And Timing Of Moth Arrival)	Rains Associated With Critical Outbreaks	Number of Degree Squares With Primary Outbreaks	Secondary Outbreaks	All Outbreaks
Seasons With Critical Primary Outbreaks In Tanzania					
1973-74	E-C Tanz (mid-late Dec)	Late start to rains (mid Dec)	9	28	34+
1974-75	NE Tanz. (late Dec)	Late start to rains (mid Dec)	7	12	19
1975-76	E-C Tanz. (mid Dec) NE Tanz. (Feb)	Late start to rains (mid Dec) Isolated rainstorms (Feb)	4	22	25
1981-82	E-C Tanz. (Nov) NE Tanz. (Dec)	Isolated rainstorms end Oct. Nov Late start to rains (mid Dec)	6	46	50+
1986-87	E-C Tanz. (Oct-Nov) NE Tanz. (Nov)	Isolated rainstorms late Oct Main rains mid Nov	15	33	39+
1987-88	E-C Tanz. (Nov-Dec) NE Tanz. (Dec)	Isolated rainstorms late Nov	17	39	50+
Seasons With Critical Primary Outbreaks In Kenya					
1980-81	E-C Kenya (Oct)	start of rains mid-late Oct (Kenya)	11	17	28
1984-85*	E-C Kenya (Oct) (early Oct)	Early start to rains in Kenya	11	35	43+
1985-86	E-C Kenya (Late Oct, mid-late Nov) SE Kenya (mid-late Nov)	Rains started late Oct	14	28	35+
Seasons 1976-77	E-C Tanz. (mid Nov) E-C Kenya (mid Nov, Jan)	Isolated rain-storm late Nov (Tanzania) Kenya rains started mid Nov Isolated rainstorm Jan	3	43	42+
Seasons with Critical Primary Outbreaks in both Kenya and Tanzania					
1978-79	NE Tanz. (Dec) E-C Kenya (mid Dec)	Rains started mid Nov	14	12	23
1979-80	NE Tanz. (Nov, Dec) E-C Kenya (Jan)	Isolated rainstorms mid Nov Late start to rains (mid Dec) Rainstorms in dry season (mid Jan)	16	34	39+
1983-84	E-C Tanz. (early Dec) Kenya coast (April, May)	Rains started early-mid Dec Long rains started April	15	30	38+
Low Seasons with No Critical Outbreaks (< 6 degree squares with outbreaks)					
1972-73	W Kenya (Dec) E-C Tanz. (May) NE Tanz. (May)	Rain started by mid Oct Long rains started April	5	0	5
1977-78	W Kenya (Feb)	Persistent rains Oct-May	1	0	1
1982-83	SE Kenya (early Oct) E-C Tanz. (end Nov-early Dec)	Rains started mid Sept, heavy to Dec	1	2	3

* 1984-85 armyworm data from Pedgley et al (1989) + severe seasons (> 33 degree squares with outbreaks).
NB. Primary and secondary outbreaks may occur in the same degree square.

(t statistic= 1.42, P= 0.18), so they could not be used to predict seasonal severity.

Since critical primary outbreaks, by definition, lead to many secondaries, identifying these should help predict seasonal severity. In Table 8 the general location and timing of critical outbreaks are listed. Critical primary outbreaks occurred in Tanzania in 10 seasons, most frequently in east-central Tanzania (seven seasons), and north-east Tanzania (seven seasons). They occurred in Kenya in seven seasons, most frequently in east-central Kenya (six seasons). These included four seasons with critical primary outbreaks in both countries. When critical primaries occurred in north-east Tanzania, they also occurred in either east-central Tanzania or east-central Kenya. Critical primary outbreaks were early outbreaks (October to December), except for one in east-central Kenya in January 1980 and those on the Kenya coast in April-May 1984.

Critical primary outbreaks in east-central Tanzania were usually associated with severe seasons (6 out of 7 occasions), as most of those in east-central Kenya were also (4 out of 6 occasions). However, critical primary outbreaks in north-east Tanzania were more closely associated with moderate (3 out of 4 occasions) than with severe seasons (4 out of 7), especially as critical primaries also occurred in either east-central Tanzania or east-central Kenya in each of these four severe seasons.

Seasons tended to be 'severe' or 'low' in both Kenya and Tanzania, but with five exceptions. The three seasons with critical primary outbreaks only in Kenya (1980-81, 1984-85 and 1985-86) were more severe in Kenya than Tanzania (when the smaller size of Kenya is taken into account). On the other hand, only one severe season with

critical primaries only in Tanzania (1986-87) failed to give rise to a severe season in Kenya. In 1973-74, the season was more severe in Kenya although the critical primaries occurred in Tanzania. This indicates that spread of outbreaks from Tanzania to Kenya is much more frequent than the reverse movement.

Figure 26 shows the annual variation in armyworm severity as measured by total numbers of degree squares with outbreaks and also by total seasonal moth catch (\log_{10}) at Muguga light trap (for comparison with Taylor (1986)). This is compared with the October-December rainfall for both Tanzania and Kenya, and with the occurrence of El Nino. The very low seasons (1972-73, 1977-78 and 1982-83) with no critical outbreaks, were at five year intervals suggesting a population cycle. However, this has not continued in recent years, with 1987-88 being a 'severe' season. Both 1977-78 and 1982-83 followed 'severe' seasons but 1972-73 followed a season that was low in Kenya, but not in Tanzania.

Muguga light trap catches followed the same trend as the number of degree squares but also showed a tendency to decrease over time. This probably reflected a decrease in efficiency of the trap, due to the rapid growth of nearby eucalyptus trees obscuring the light to the north of the site. As previously described, El Nino episodes preceded or coincided with heavy October to December rainfall in 1972, 1977 and 1982. Rainfall was slightly above average in October-December 1986 following the 1986 El Nino but armyworm outbreak severity remained high in both 1986-87 and 1987-88.

A regression of the October to December rainfall index for Kenya and Tanzania against number of degree squares with outbreaks, for all seasons (Figure 27) showed a significant inverse linear relationship ($R = -0.54$,

Figure 26. Time-section of the variation in the seasonal severity of armyworm, measured by degree-squares infested by outbreaks and by Muguga light trap catches of moths, compared with an index of October-December rainfall and the occurrence of El Nino.

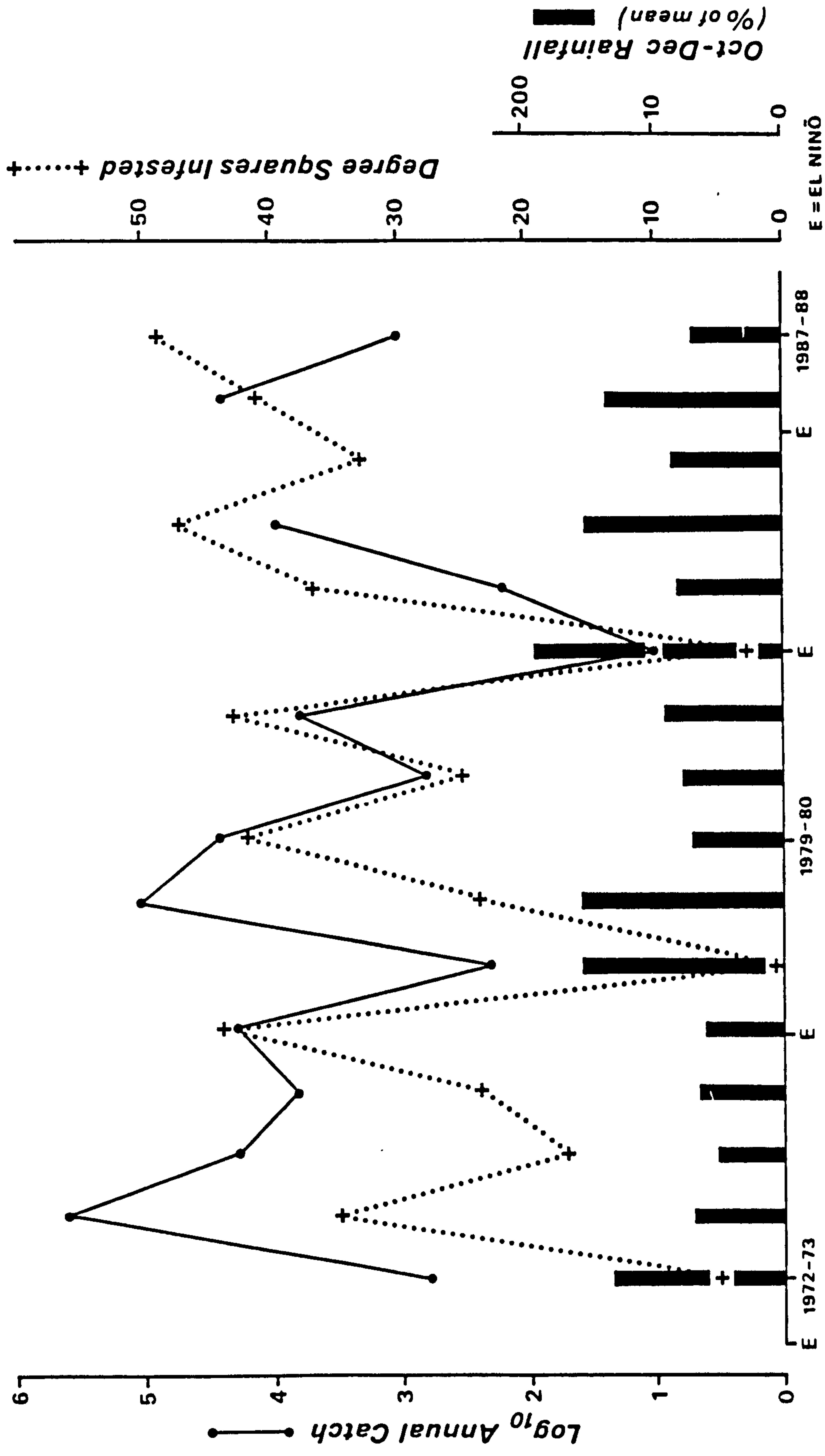
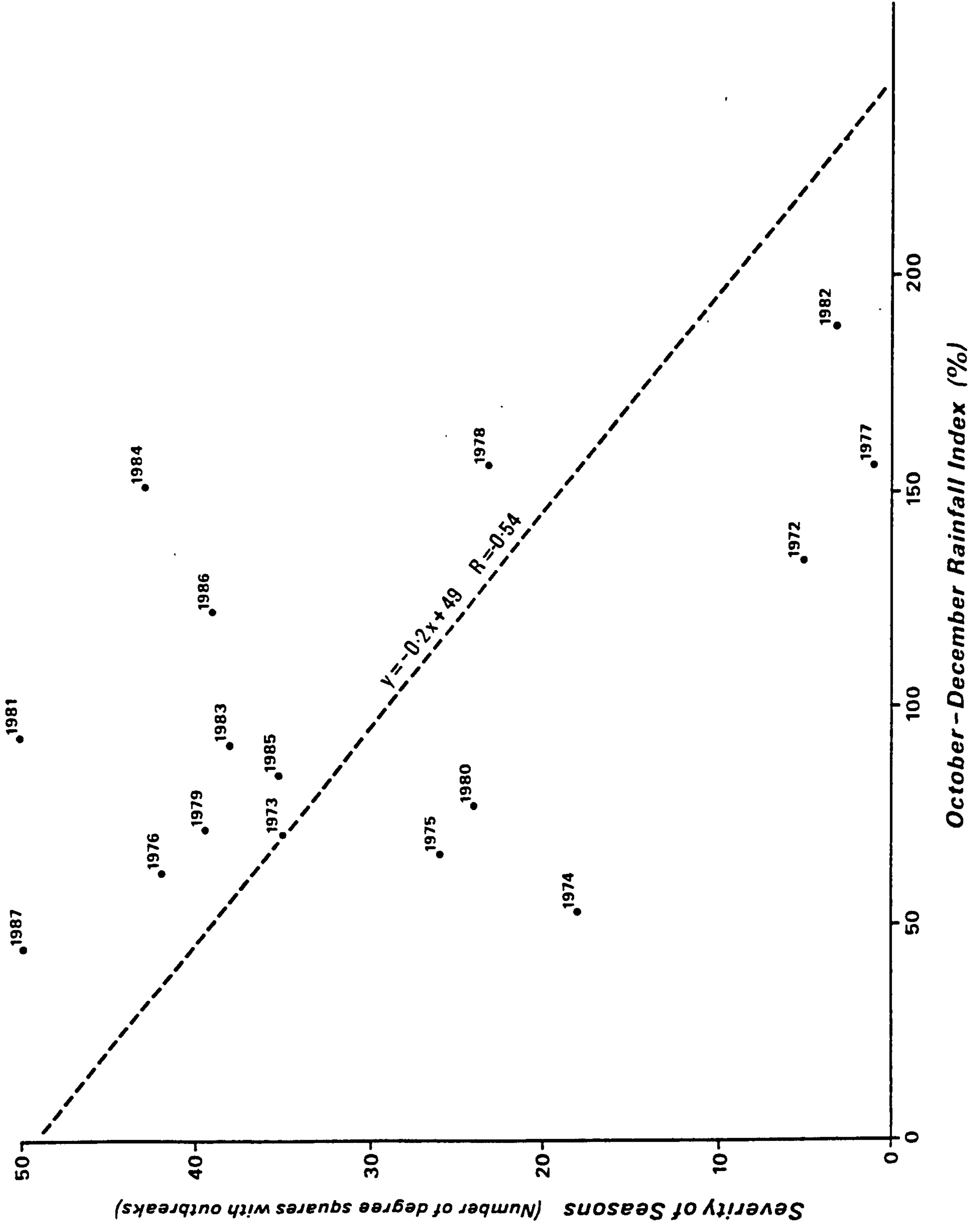


Figure 27. Regression of the severity of the armyworm season (degree squares infested by outbreaks) on the October-December rainfall index.



$P < 0.05$). However, this depended strongly on the three very low armyworm seasons (1972-73, 1977-78 and 1982-83), which all had very high October-December rainfall indices ($>130\%$) and one very severe season (1987-88) which had a very low rainfall index. Two seasons, 1974-75 and 1984-85, did not fit the general trend, being much less severe and more severe, respectively than predicted by the regression. In 1974-75, outbreaks failed to spread westwards from east-central Tanzania in spite of dry conditions, while in 1984-85, outbreaks in Kenya were very severe in spite of heavy rains. In 9 out of 16 seasons, rainfall was within about 30% of the mean and, in this range, there was no clear inverse correlation between rainfall and seasonal outbreak severity.

The outliers of the regression suggest that seasonal relationships between rainfall and outbreak occurrence may have been masked by considering Kenya and Tanzania together. Numbers of degree squares with outbreaks in Kenya were, therefore, compared with rainfall indices derived from three stations in the primary outbreak area of southeast-central Kenya (Voi, Makindu and Nairobi)(Figs 28,29). Weak inverse correlations were found for both short rains (October-December)($R = -0.51$, $P = 0.04$) and the previous long rains (March-May)($R = -0.4$, $P = 0.14$), although the latter was not significant. The correlation for the short rains was improved ($R = -0.69$, $P = 0.004$) when the exceptional year 1984-85 was removed. As found by Haggis (in press), a stronger inverse association was found when data were categorized as 'high' (above the mean) and 'low' (below the mean). Then using Fisher's exact test, Kenya outbreak severity was significantly ($P < 0.05$) inversely associated with both short rains and previous long-rains rainfall.

Similarly numbers of degree squares with outbreaks in Tanzania were compared with indices of rainfall from four

Figure 28. Regression of Kenya outbreak severity (number of degree squares infested) on the October-December rainfall index for east-central Kenya.

Kenya outbreak severity and October -
December rains in E-C Kenya

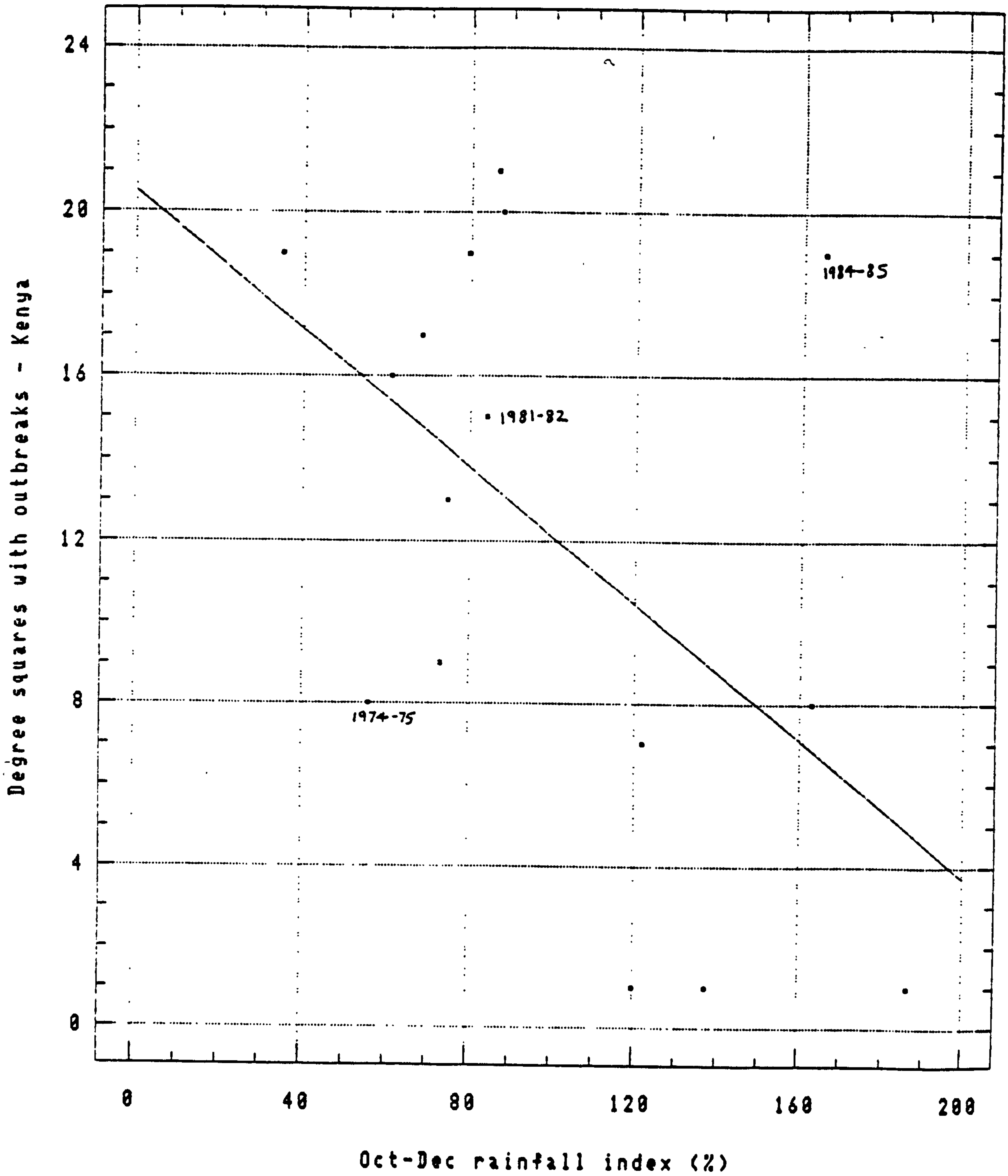
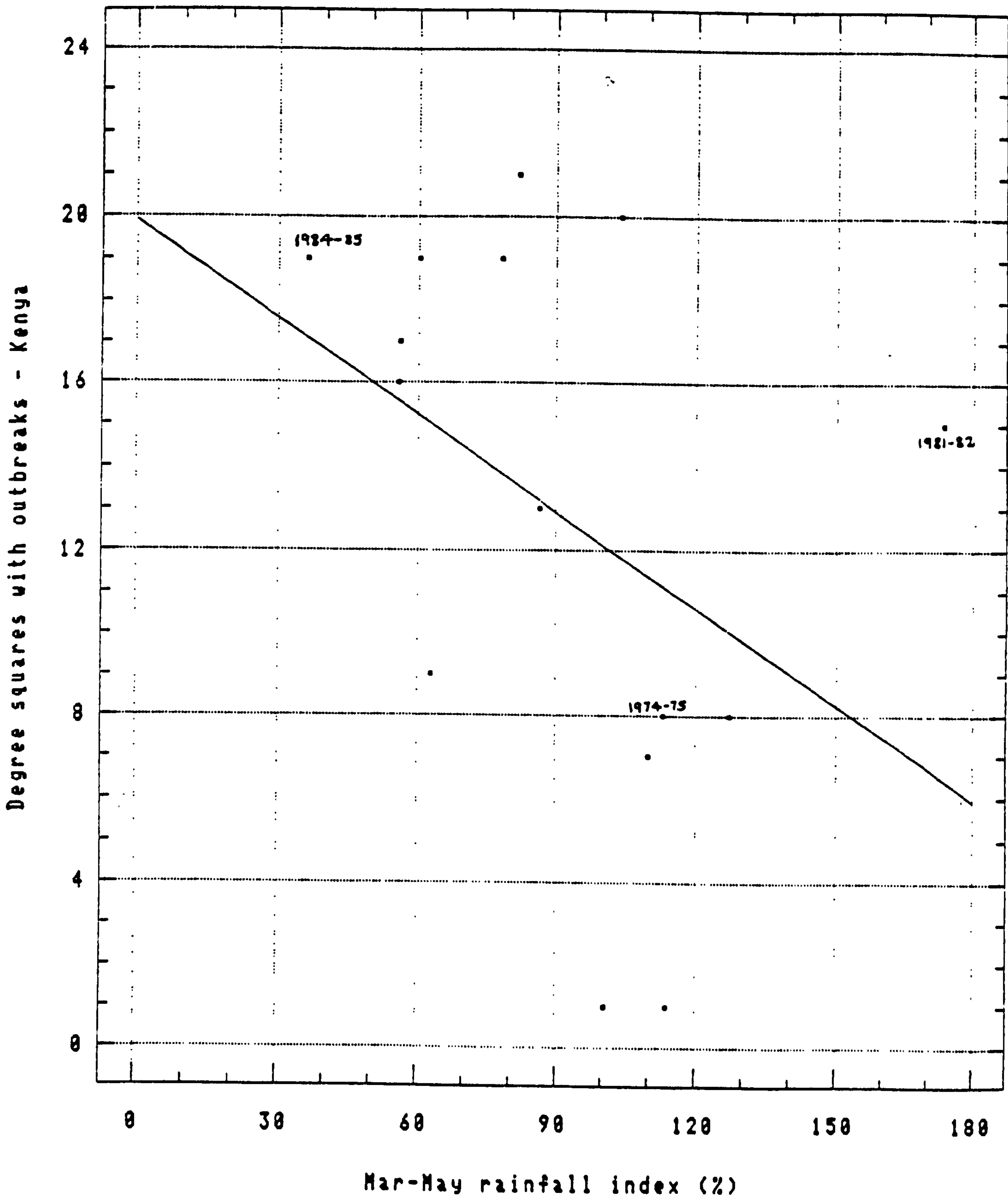


Figure 29. Regression of the Kenya outbreak severity (number of degree squares infested) on the previous March-May rainfall index for east-central Kenya.

Kenya outbreak severity and March -
May Rains in E-C Kenya



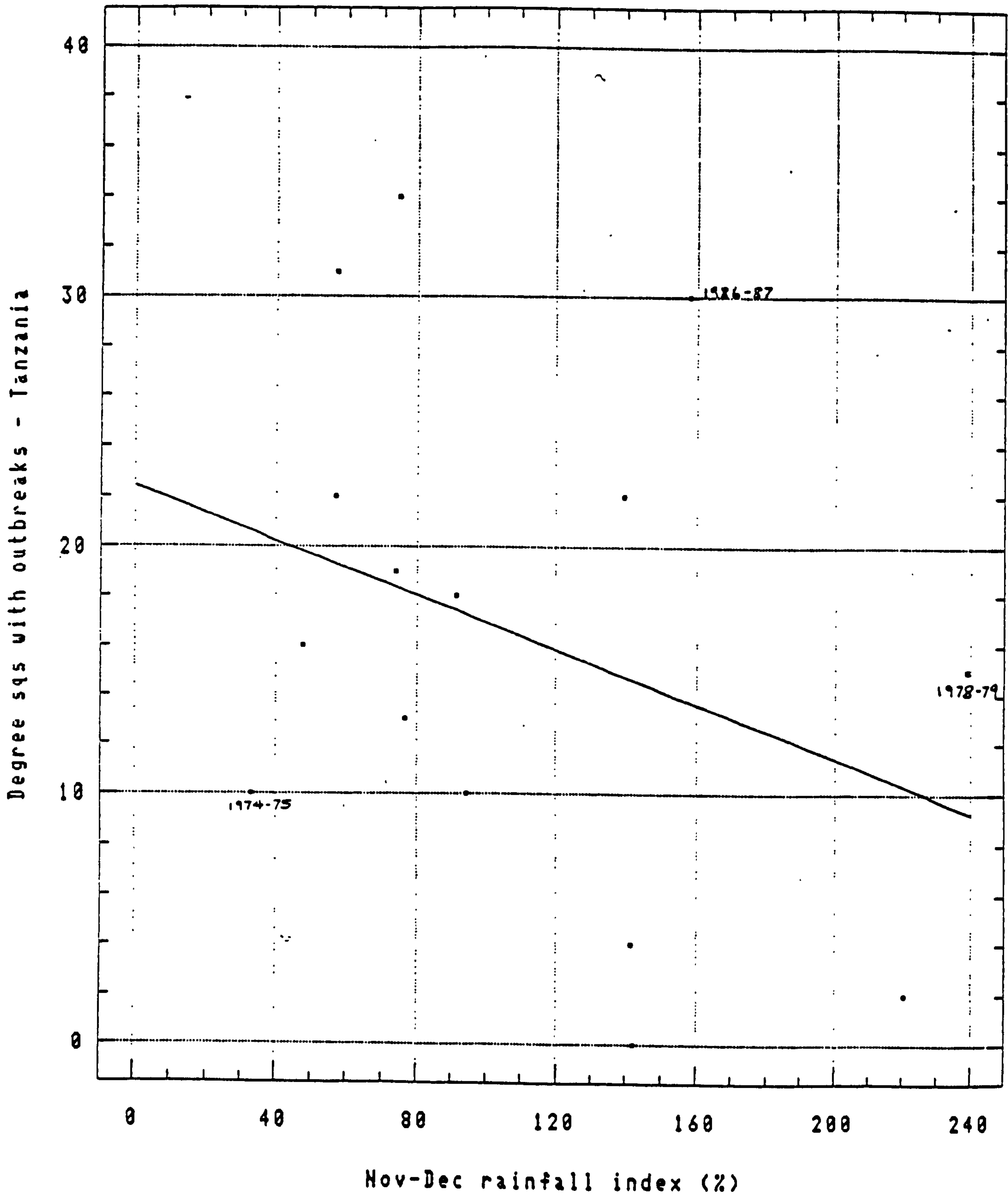
stations in the east-central and north-east Tanzania primary outbreak areas (Morogoro, Dodoma, Arusha and Same). For 15 seasons (no rainfall data were available for 1984-85), there was a weak, insignificant, inverse correlation between outbreaks and short rains rainfall ($R=-0.33$, $P=0.23$) (Fig 30) and there was no correlation for the previous long-rains. Considering categories above and below the mean (as for the Kenya data) an inverse association was apparent for the short rains but this was not significant ($P=0.16$). Again, there was no association for the previous long rains.

East-central Kenya had six seasons with early primary outbreaks and ten without, suggesting that their occurrence might be forecast from short-rains or previous long-rains rainfall. Seasons were divided into those with early primary outbreaks in east-central Kenya and those without. Early-season rainfall indices for southeast-central Kenya (as above) were compared for the two sets of seasons by both the parametric Difference of Means test and by non-parametric Comparisons of Ranks. No significant differences were found for either test, although only one season with early primary outbreaks in east-central Kenya had above average rainfall in the previous long-rains.

From the analyses of individual rainstorms and outbreaks in particular seasons, it was observed that seasons with many *Spodoptera exempta* outbreaks often had rainstorms separated by dry periods of about 10-14 days, in the short-rains. This was true for both seasons with heavy short-rains (e.g.1984-85) and those with light short-rains (e.g.1987-88). Armyworm outbreaks were often associated with rainstorms but these were preceded and followed by dry periods (Chapter 7). On the other hand, very low armyworm seasons had rain on many days during the short-rains.

Figure 30. Regression of Tanzania outbreak severity (numbers of degree squares infested) on the November-December rainfall index for Tanzania primary outbreak areas.

Tanzania outbreak severity and November-December rains in primary outbreak areas



(d) Discussion

The results of this study support those of previous studies that found inverse relationships between seasonal armyworm severity and short-rains rainfall (Tucker 1984b, Haggis-in press, and Harvey-unpublished) and also, for Kenya, with the previous long rains (Haggis-in press). Seasonal armyworm forecasting for Kenya might be improved by using both short-rains and the previous long-rains rainfall. The present results indicate that the inverse association with short-rains rainfall is weaker for Tanzania than for Kenya (although this relationship has been confirmed by Harvey, unpublished), and there was no relationship with the previous long-rains. Predictions of armyworm seasons in Kenya from the previous long-rains are likely to be less accurate in seasons in which outbreaks spread from Tanzania than in those when outbreaks originate from Kenya. It may be possible to use the distribution of rainfall *within* the short-rains to improve seasonal forecasts.

The causes of the inverse relationship between armyworm outbreak numbers and rainfall are likely to be a combination of improved food-plant quality, either because grasses are younger or because they have a higher nitrogen content, and lower larval mortality, probably due to lower incidence of virus attack and possibly of other pathogens (eg fungal diseases) and parasites. Direct monitoring of food-plant quality using the NOAA satellite and the NDVI, has been mentioned but not investigated directly. Robinson's (1991) work shows that NDVI can be used to monitor monthly vegetation changes that are associated with the general distribution of armyworm outbreaks, and it should therefore be possible to use NDVI, in addition to rainfall data to compare seasons and forecast seasonal severity. The use of NDVI for locating individual outbreaks has not been

demonstrated but it may be possible to use Local Area Coverage (1.1km resolution) NOAA data to forecast likely locations of primary armyworm outbreaks early in the season.

Results from studies of individual rainstorms and outbreaks, presented in Chapter 7, also suggest that seasons are likely to be severe when rainstorms are separated by dry spells and very light when rains are more continuous, probably due to high larval mortality in conditions of high humidity and poor sunlight which lead to a high incidence of disease.

Seasonal armyworm forecasts must therefore consider both total seasonal rainfall and the distribution of rainfall on a daily basis.

CHAPTER 7. FORECASTING SPODOPTERA EXEMPTA OUTBREAKS FROM RAINSTORM DISTRIBUTION

(a) Introduction

Evidence for the association of African armyworm outbreaks with rainstorms and, in particular, rainstorm low-level outflows, has been direct, from radar observations (Pedgley et al 1982, Riley et al 1983) and indirect, from statistical and biogeographical analyses (Tucker and Pedgley 1983, Pedgley et al 1989). Tucker and Pedgley (1983) found a significant association between outbreak oviposition dates and rainstorms for the period January to March 1974 and 1975, but not for April and May. Pedgley et al (1989) found that primary and secondary outbreaks in Kenya and Tanzania from October to December 1985 were associated with rainstorms, except for some low-density (<10 larvae m^{-2}) outbreaks that derived from oviposition during a dry spell. Mechanisms likely to cause moth concentration with rainstorms have been discussed by Pedgley (1982, 1990) and in this thesis in Chapter 2.

The present work has used an assumption that, within an estimated moth arrival period for an outbreak, armyworm moths were more likely to have been concentrated, prior to oviposition, on nights with rainstorms than on other nights. This assumption helps refine the likely moth arrival dates. The original, unrefined armyworm data could be used to extend previous analyses by investigating the statistical association between outbreaks and rainstorms for up to thirteen seasons, especially for the period October to December. This would help determine whether African armyworm outbreaks can be forecast reliably using rainfall data either to supplement moth trap data or, in the absence of trap data, on its own.

A major constraint on the use of rain-gauge data for forecasting armyworm outbreaks is that, to be useful, data must be available within a week of rainstorm occurrence. Except for data from widely spaced synoptic meteorological stations, rain-gauge data are not available quickly enough. However, satellite data can be obtained almost immediately, using a ground receiving station and the European Space Agency Meteosat geostationary satellite. This has the advantage that it monitors the whole of Africa every half hour. The use of Meteosat imagery for identifying rainstorms associated with armyworm outbreaks was investigated by Garland (1985) using data archived by Dundee University and Imperial College, UK. She concluded that most armyworm outbreaks appeared to be associated with areas of active convection but that the relationship between outbreaks and heavy rainfall remained unclear. She considered that digital Meteosat data had a future place in the procedure for forecasting armyworm outbreaks as an addition to other meteorological data, but only if an existing forecasting facility had real-time access to Meteosat data and powerful processing facilities. In September 1988 this became possible, when a low-cost Meteosat Primary Data User Station (PDUS) was installed at the Regional Armyworm Forecasting Service, DLCO-EA, Nairobi. The system, which consists of a small (2m) dish antenna and a purpose-built receiving unit linked to a personal desk-top computer (minimum 640 Kbyte RAM, 30 Mbyte hard disk and extended graphics card), was developed by Bradford University Research Limited-BURL (now Bradford University Remote Sensing Ltd-BURS). The 'Autosat' receiving and processing software, was also developed by BURL, in conjunction with the University of Reading and the Natural Resources Institute (BURL 1991). Primary (digital) data are received directly from the satellite as it scans the Earth below, together with calibration data which enable radiance values to be automatically

converted to meaningful figures (temperatures in the case of infra-red data). This contrasts with Secondary Receiving Systems which receive data that has been pre-processed at a ground station and re-broadcast via Meteosat. Secondary data are easier to receive and provide pictures, but are not calibrated. BURL Primary Data User Systems have now been installed in about eight African countries, in Jordan and in Britain, as part of the joint Natural Resources Institute, BURL, Reading University and Silsoe University LARST (Local Applications of Remote Sensing Techniques) project. They are now generally known as LARST systems.

Meteosat data have now been used for over three years in armyworm forecasting and have been judged very useful by forecasters. Mwandoto (1993) has investigated relationships between Meteosat infra-red imagery, rainfall and armyworm forecasts but further work is needed to evaluate the success of this method. It was therefore decided, at a late stage in the present work, to carry out a limited study to evaluate the use of Meteosat data for African armyworm forecasting.

The use of NOAA satellite data to monitor vegetation greenness as a possible alternative means of forecasting armyworm outbreaks has been extensively investigated by Robinson (1991). Aspects of his work have already been mentioned and will be discussed in relation to the present study on the use of Meteosat cold-cloud imagery .

In the present work, the use of rainfall data for forecasting the location of African armyworm outbreaks will be assessed using:

- (i) rain-gauge and outbreak data for the period 1972-88;
- (ii) Meteosat imagery and outbreak data for the period October to December 1992.

(b) Rainstorms and outbreaks 1972-88

(i) Data and Methods

Rain-gauge data obtained for the analysis of outbreaks in the 1972-73 to 1987-88 armyworm seasons (which excluded 1984-85) were used. Data were daily (24 hour) totals for gauges within about 50km of outbreak sites for a total of 104 outbreaks (or groups of outbreaks), including primary outbreaks for the whole season and secondary outbreaks for October to February. Late-season secondaries were not included because of frequent overlapping generations and because rainfall data had been obtained only for particular, significant outbreaks which were therefore a biased sample. As discussed on pp 48,59, although night-time-only rainfall data would have been preferable, 24 hour totals gave a reasonable indication of the incidence of evening and night-time rainstorms, because most storms occurred from late afternoon to midnight. The methodology was based on Tucker & Pedgley (1983). For each armyworm outbreak, the moth arrival period was estimated based on larval instars or head-width, together with development tables and/or the regression (described in Chapter 2) but without any correction based on rainstorm occurrence. Moth-arrival periods were then standardised to an eleven-day period centred on the most likely moth-arrival date. This period was chosen because most estimates of moth arrival had error terms of about +/- 5 days. 'Rainstorm days' were defined as those with >10mm of rainfall, an amount likely to be associated with a vigorous convective rainstorm in eastern Africa. As there were rarely rain-gauges at the actual outbreak site, periods with a 'high' likelihood of a rainstorm at that site were defined as ones with:

at least one day with >10mm rain at a gauge within approximately 10km;
or daily totals of >10mm rain recorded from at least half the rain gauges within 50km of the outbreak site.

When rainstorms were less frequent or absent, the likelihoods were considered 'moderate' or 'low'.

The distribution of rainstorms over periods of about a month, centred on the most likely moth-arrival date, were then examined by considering three 11-day periods, before, during and after the estimated moth-arrival period. The frequency of a high likelihood of rainstorms was compared for the three 11-day periods, using Chi square analysis, for primary and secondary outbreaks separately.

(b) Results (Table 9)

Eighty percent of the 104 outbreaks had a 'high' likelihood of rainstorms at or near the site during the estimated moth arrival period, compared with 38% and 50% for the previous and subsequent 11-day periods respectively. This suggests a positive association between moth-arrival before outbreaks and rainstorms.

Considering the three 11-day periods, before, during and after moth-arrival, there are 8 possible combinations when periods with a 'high' probability of a rainstorm are compared with those with a 'moderate or low' probability of a rainstorm i.e.

Frequency of a high probability of a rainstorm in the 11-day period for:

a) Primary outbreaks

	B	D	A	<u>Total</u>
	<u>11-days</u> <u>pre-MAP</u>	<u>Moth arrival</u> <u>period (MAP)</u>	<u>11-days</u> <u>post-MAP</u>	
Only in given period	2	6	2	10
All but given period	14	2	4	20
Total	16	8	6	30
Expected values	5.3	2.7	2.0	
	10.7	5.3	4.0	

Chi square = 9.38** (probability < 0.01)

b) Secondary outbreaks

	B	D	A	<u>Total</u>
Only in given period	4	12	2	18
All but given period	12	0	10	22
Total	16	12	12	40
Expected values	7.2	5.4	5.4	
	8.8	6.6	6.6	

Chi square = 21.15*** (probability < 0.001)

Table 9. Comparison between the likelihood of rainstorms in African armyworm outbreak moth arrival periods and in the preceding and subsequent 11-day periods.

Before	During	After
1	1	1
1	1	0
1	0	1
0	1	1
1	0	0
0	1	0
0	0	1
0	0	0

(where 1 represents presence and 0 absence).

The first and last combinations give us no information useful for forecasting the occurrence of armyworm outbreaks in any given month. The remaining six combinations can be set up as a two-way table comparing frequencies of high likelihoods of rainstorms only in the given period, with frequencies of rainstorms in all but the given period. Table 9 shows the frequencies for primary and secondary outbreaks separately for all outbreaks where rainfall data were available for all three 11-day periods. The expected values for a random distribution and the resulting Chi-square values are included, but occasions with either 'rainstorms' or 'no rainstorms' in all three periods are excluded.

For both primary and secondary outbreaks, the distribution was highly significantly different from that which would be expected by chance. When rainstorms were likely to have occurred in only one of the three periods, they most frequently occurred in the estimated moth arrival period (60% of occasions for primary outbreaks and 67% of occasions for secondaries). When rainstorms occurred in two out of three periods, the 'dry' periods were most likely to be before the moth-arrival period, especially for primary outbreaks (70% of occasions). Overall 20 out of 30 primary outbreaks and 24 out of 40 secondary outbreaks were associated with periods with rainstorms following an 11-day spell without such storms.

For secondary outbreaks, dry 11-day periods following rainstorms in both the moth-arrival period and the preceding 11-days were also quite frequent (45% of occasions) and 34 out of 40 secondary outbreaks had rainstorms in moth-arrival periods preceded or followed by dry periods. The frequency of 'dry' moth-arrival periods preceded and followed by periods with rainstorms was very low (10% for primaries and 0% for secondaries).

(iii) Discussion

The higher than expected associations between outbreak moth arrival periods and high likelihoods of rainstorms gives support to the monitoring of rainstorms for forecasting armyworm outbreaks from October to February. For primary outbreaks, the first rainstorm following a 'dry' period is a good indication that an armyworm outbreak might occur (67% chance based on present data). For secondary outbreaks such a forecast would have a 60% chance of being correct but this would be increased to 85% if the period following the moth arrival period was 'dry'.

The results extend, to the period October to December, those of Tucker & Pedgley (1983), who found significant associations between outbreaks and rainstorms for January- March but not for April-May. It was not possible to extend the present analysis to the period March-June because rainstorm data were only available for a biased sample of outbreaks. Since 74% of primary outbreaks occurred in the period October to December, the occurrence of rainstorms following dry periods is likely to be particularly useful for forecasting primary outbreaks, as found by Pedgley *et al* (1989) for October-December 1984.

For secondary outbreaks from October to February (possibly March), the best forecast is obtained by also considering the period following the moth-arrival period. The probability of a secondary outbreak is increased when the moth-arrival period (and oviposition) is followed by a 'dry' period. This is likely to be because secondary outbreaks are more susceptible to mortality from virus infection or parasites that increases with moist conditions, than primary outbreaks, especially if the outbreak occurs near the parent outbreak.

(c) Satellite monitoring of rainstorms for armyworm outbreak forecasting

(i) Data

As this study was started after the author's return to Britain, data from the Meteosat meteorological satellite were received and processed at the Natural Resources Institute, UK, rather than in Nairobi. Meteosat maintains a geostationary orbit at an altitude of 35400 km above the equator, over the Greenwich Meridian. From this position, it monitors the whole of Africa and most of Europe at half-hourly intervals and broadcasts to any receiving stations in these areas. Thus receivers linked to dish antennae directed towards the satellite, located at NRI, UK and DLCO-EA, Nairobi, could receive the same data.

Meteosat radiometers scan the Earth in three wavebands, visible (0.4 - 1.1 μm) which records reflected sunlight, thermal infra-red (10.5 - 12.5 μm) which records emitted long-wave radiation and near infra-red (5.7 - 7.1 μm) which records radiation in the water vapour absorption channel (Milford 1989). Visible and infra-red channels are widely used for monitoring clouds and rainfall. In visible wavelengths, high reflectivity (brightness)

indicates thick clouds that are likely to give heavy rain, but monitoring is only possible in daylight. In infra-red wavelengths, emitted radiation is directly related to the temperature of the emitting body, which can be estimated assuming that it is emitting as a black-body (without long-wave reflection). Cloud-top temperatures are lower than ground temperatures by an amount determined by the environmental lapse rate and the height of the cloud. Large convective clouds (cumulonimbus and cumulo-congestus) have cloud-top temperatures below -30°C (243K) and, in the tropics, often below -50°C (223K) and down to -70°C (203K). The duration of the presence of such cold clouds is related to total rain falling from the clouds, and therefore cold-cloud duration has been widely used to estimate rainfall in areas where convective rainfall predominates, as in much of the tropics (Arkin & Meisner 1987, Milford & Dugdale 1989). For the Sahel of west Africa, cloud-top temperature thresholds of -60°C or -50°C have been found to give the best rainfall estimates (Jobard & Desbois 1992) while, in Ethiopia and Somalia, thresholds of -50°C or -40°C are best (Milford & Dugdale 1991).

Rainfall estimates are usually made for 10-day periods, which reduces errors caused by short-lived, non-precipitating convective clouds, and cirrus outflows from cumulonimbus that may spread well away from the main cloud mass. Errors may also be reduced by using combinations of infra-red and visible imagery (Martin & Howland 1986, Porcu & Levizzani 1992) but, besides doubling the amount of data to be processed, this is only feasible during daylight.

The maximum resolution of the Meteosat data is determined by the pixel size, which is about 5 x 5 km vertically below the satellite but increases for oblique (off-nadir) views, where resolution is therefore poorer. The LARST

Meteosat PDUS collects an image of 512 x 512 pixels, equivalent to approximately 20° latitude by 20° longitude. The area collected for armyworm forecasting in East Africa is centred on 1°S, 33°E (in Southern Uganda). It extends from central Ethiopia to northern Mozambique and from Somalia and the Indian Ocean to Zaire, and includes all of Kenya, Tanzania and Uganda. The satellite angle of view is 36° from the vertical over eastern Somalia. Correspondingly, the pixel size increases from a width of about 6km over Uganda and Western Kenya to 9km in Eastern Somalia.

African armyworm data, comprising outbreak reports and trap catches for October 1992 to January 1993, were obtained from weekly summaries and forecasts for Kenya, issued by the Kenya armyworm forecasting service. Outbreak data for the same period for Tanzania were obtained from a summary supplied by the Regional Armyworm Forecasting Service, but originating from the Tanzanian Pest Control Services.

(ii) Methods

For African armyworm forecasting, the locations of convective rainstorms on particular nights were needed. This required monitoring cold-cloud occurrence on separate nights, rather than integrating over 10-days, as would be required for estimating the actual amount of rainfall. Therefore the software was set up to receive half-hourly infra-red images from 1800 to 0600 local time and to construct nightly (12 hours) composite maps of cold cloud duration. These show the number of hours that temperatures of less than the chosen threshold (usually -50°C) were present for each pixel (or data unit). The threshold was based on Milford & Dugdale (1991). Pilot studies in eastern Africa (Tucker-unpublished) indicated that this threshold picked out large rainstorm complexes

very well, although no systematic calibration was done against rain gauge data. Subsequently Mwandoto (1993) compared Meteosat infra-red imagery with point rainfall data. Using thresholds of -15° , -35° and -60°C , he concluded that -35°C gave the best correlation with point rainfall. Mwandoto also tried to identify the size of cloud cluster most often associated with armyworm outbreaks and concluded that medium or large clusters were more important than small ones of less than 20km diameter.

For the present study, nightly, cold-cloud duration images for October to December 1992 were automatically calculated. These were archived onto floppy disks and were also printed out. A few individual infra-red images were also archived onto floppy disk for later comparison with the cold-cloud images.

A methodology similar to that currently used for regional armyworm forecasting at DLCO-EA was adopted so as to assess the value of forecasts based on Meteosat data alone. A subset of 33 degree squares covering the main primary outbreak areas in Kenya and Tanzania was chosen (Fig 31). Nightly cold-cloud duration images were examined and, for each forecasting week, degree squares with cold cloud present for one or more hours, on one or more nights, were recorded. Armyworm outbreaks were mapped by location and reporting date and the distribution of outbreaks was then summarised using the degree square in which outbreaks occurred and the week in which it was estimated that moth-arrival prior to oviposition took place. Moth-arrival was estimated using development tables and regression, as before (p 55).

The frequency with which outbreaks and rainstorms occurred in the same degree square and week was compared with the frequency of each occurring alone and with the

frequency of neither occurring, using the Chi square statistic to test the significance of any association. Outbreak locations were then plotted on nightly cold-cloud duration maps to see if outbreaks were associated with any particular features of the cold-cloud clusters, and whether any such relationships were consistent with the hypothesized mechanisms for concentrating flying moths. Since the cold cloud distribution maps were integrations over 12 hours, it was not possible to relate outbreaks to the particular stages in development and dissipation of the rainstorms. The maps indicated the maximum extent of cold cloud on that particular night, which may have been considerably wider than the area of heavy rain. This use of a low threshold (-50°C rather than -40 or -35°C) reduced the area covered and the likely errors introduced by nightly integration.

(c) Results (Tables 10,11, Figs 31-36)

The first armyworm outbreaks of the season were reported in Meru and Makueni districts of east-central Kenya with estimated moth arrival at the beginning of November. In Kenya, outbreaks then occurred on the coast, at Mariakani, Kilifi and Kwale; in Taita and Taveta districts of south-east Kenya; and in Machakos and Makueni districts of east-central Kenya. All had estimated moth arrival dates in mid-late November. In Tanzania, the first outbreaks occurred in Morogoro district, east-central Tanzania, with estimated moth arrival in early-mid November (Table 10). Outbreaks followed in Kilimanjaro and Arusha regions of northern Tanzania (estimated moth arrival in mid November) and in Tanga region of north-east Tanzania (estimated moth arrival at the end of November). All of these outbreaks were primary because there were no known outbreak sources and there was less than one generation in timing between them. No further outbreaks were reported in Kenya until

Outbreak location Degree square Estimated moth arrival

KENYA

Tigania, Meru D.	0-1°N 37-38°E	28/10 - 6/11/92
Makueni District	1-2°S 37-38°E	1/11 - 9/11/92
Mariakani (coast)	3-4°S 39-40°E	18/11 -21/11/92
Kilifi (coast)	3-4°S 39-40°E	16/11 -25/11/92
Taveta District	3-4°S 37-38°E	16/11 -25/11/92
Mwatate, Taita dist.	3-4°S 38-39°E	16/11 -25/11/92
Kwale D. (coast)	4-5°S 39-40°E	19/11 -28/11/92
Masii, Machakos dist.	1-2°S 37-38°E	11/11 -25/11/92
Matiliku, Makueni D.	1-2°S 37-38°E	11/11 -25/11/92

TANZANIA

Kingolwira, Morogoro	6-7°S 37-38°E	3/11 -13/11/92
Arumeru, Arusha dist.	3-4°S 36-37°E	10/11 -20/11/92
Mwanga, Kilimanjaro	4-5°S 38-39°E	10/11 -20/11/92
Babati, Arusha dist.	4-5°S 35-36°E	10/11 -20/11/92
Rombo, Kilimanjaro	3-4°S 37-38°E	10/11 -20/11/92
Same, Kilimanjaro	4-5°S 37-38°E	19/11 -29/11/92
Lushoto, Tanga D.	4-5°S 38-39°E	23/11 - 3/12/92

Table 10. Location and timing of primary armyworm outbreaks in November 1992

Degree square	Week			
	2-8/11	9-15/11	16-22/11	23/29/11
0-1N, 37-38E	0*	1	0	0
0-1N, 38-39E	0	1	0	1
0-1S, 37-38E	0	1	0	0
0-1S, 38-39E	0	1	0	0
1-2S, 36-37E	0	0	0	0
1-2S, 37-38E	0*	0	1*	0
1-2S, 38-39E	0	2	1	1
2-3S, 36-37E	0	0	3	0
2-3S, 37-38E	0	0	1	1
2-3S, 38-39E	0	1	2	2
3-4S, 35-36E	0	1	4	0
3-4S, 36-37E	0	0	4*	0
3-4S, 37-38E	1	1	2*	1*
3-4S, 38-39E	1	1	4*	0
3-4S, 39-40E	0	2	3**	1
4-5S, 35-36E	0	1	2*	1
4-5S, 36-37E	0	1	3	1
4-5S, 37-38E	0	1	3	1*
4-5S, 38-39E	0	1	5*	1*
4-5S, 39-40E	0	0	4*	1
5-6S, 35-36E	0	1	4	0
5-6S, 36-37E	0	1	4	0
5-6S, 37-38E	0	0	4	0
5-6S, 38-39E	0	0	5	0
6-7S, 35-36E	0	0	4	0
6-7S, 36-37E	0	2	6	0
6-7S, 37-38E	0	2*	5	1
6-7S, 38-39E	0	1	5	0
7-8S, 35-36E	0	0	4	0
7-8S, 36-37E	0	2	4	0
7-8S, 37-38E	0	1	4	1
7-8S, 38-39E	0	1	3	1
8-9S, 36-37E	0	1	4	0

KEY

* Primary outbreak (moth arrival)

Table 11. Number of rainstorms per degree square per week in November 1992 in relation to the occurrence of primary armyworm outbreaks.

February (estimated moth arrival in January). In Tanzania, however there were further outbreaks in Kilimanjaro, Arusha, Dodoma and Morogoro regions in December which were almost certainly secondaries, derived from the November outbreaks.

Table 11 lists the number of rainstorms, derived from nightly images of cold-cloud duration, per degree square for each week in November 1992. Armyworm outbreaks are indicated by the degree square in which they occurred and the week of estimated moth arrival.

The incidence of rainstorms and primary outbreaks was then compared and the association between them was tested by the Chi square statistic (Table 12). There was a highly significant positive association ($\chi^2 = 7.55$, $P < 0.01$).

Out of 15 primary outbreaks, or groups of outbreaks (listed in Table 10), 13 were associated with rainstorms in the same degree square. The exceptions were the first two outbreaks of the season in Meru and Machakos districts of Kenya which had estimated moth arrival dates between 26 October and 8 November, when rainstorms were very infrequent. One primary outbreak, in Morogoro region, was associated with isolated rainstorms in week 9-15 November, and three with isolated rainstorms in week 23-29 November. The remaining nine outbreaks were all associated with frequent rainstorms in week 16-22 November.

There were 15 primary outbreaks but 69 rainstorms in the subset of 33 degree squares considered. Because of this and in spite of the strong positive association, forecasting outbreaks from rainstorm occurrence alone, even for the primary outbreak area alone, would have produced 54 incorrect positive forecasts. In any one week

		Rainstorms/week		Total
		Present	Absent	
Primary Outbreaks	Present	13	2	15
	Absent	56	61	117
	Total	69	63	132

$$x^2 = \frac{(O - E)^2}{E} = 7.55$$

For 1 degree of freedom significant at 0.01 level

Table 12. Comparison between rainstorm occurrence (from Meteosat data) and armyworm outbreak moth arrival periods in November 1992.

the percentage of correct forecasts was between 0 to 31%. From a practical point of view, the number of degree squares that might have been surveyed without finding an outbreak would have varied from 28 to 32, without any forecasts based on rainstorms derived from Meteosat data. With such forecasts this would have been reduced to 2 degree squares, before the main rains, to 22 at the height of the short rains. These results indicate that forecasts are most useful when rainstorms are scattered. Although the two incorrect negative forecasts occurred at the very beginning of the season, the effort wasted in looking for outbreaks that did not occur would have been small.

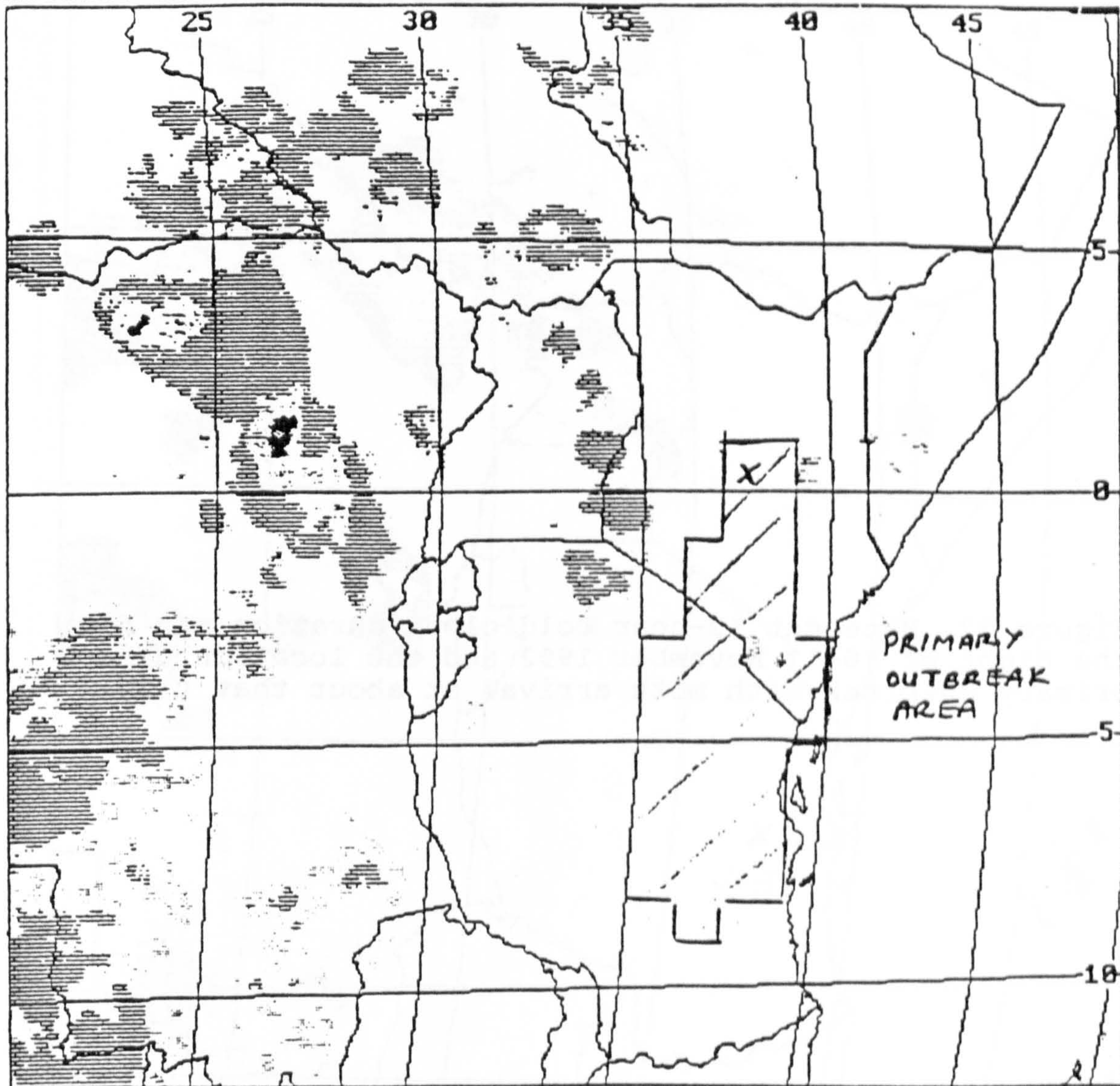
The locations of individual armyworm outbreaks were then plotted on cold-cloud duration maps for the night on which moths were most likely to have been concentrated by rainstorms (Figs 31-36). The maps were examined to see if a more precise relationship between outbreaks and rainstorms (as identified from the -50°C cold cloud threshold) could be found than from weekly summaries.

Although there was no close association between the Meru outbreak and a rainstorm, there was an isolated patch of cold cloud about 120 km to the east, possibly within range of a strong downdraught outflow (Fig 31). Alternatively there may have been a zone of wind convergence caused by a katabatic (downslope) wind from Mount Kenya to the east, meeting the dominant easterly flow. The first Morogoro outbreak was associated with the remnants of a cyclonic storm moving inland from the Indian Ocean (Fig 32). On 14, 16, 18 and 27 November outbreaks were associated with the edges of cold cloud clusters, mostly in northern Tanzania and eastern Kenya (Figs 33-36). Five were just upwind and six downwind of the centre of the cloud cluster. This suggests that the hypothesis that moth concentration is associated with

Figure 31. Meteosat 12-hour cold-cloud duration map for the night of 2-3 November 1992, also showing the primary outbreak area used for the analysis and the location of a primary outbreak with moth arrival at about that time.

HALF DAY COLD CLOUD DURATION MAP.

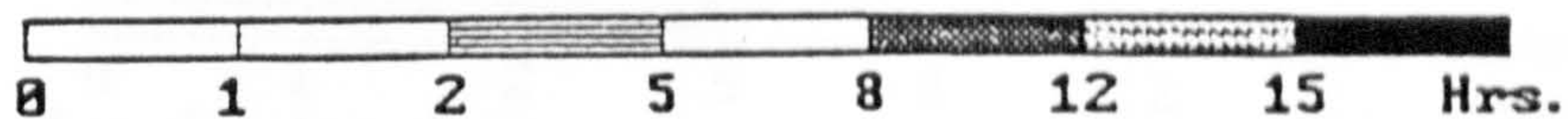
REGION: EASTERN AFRICA PRINTED AT: NRI



Start time: 15:00 02/11/1992

Filename: UGCHF2BF.CCD

COMMENTS:



x Outbreak Location

IMAGE USAGE INFORMATION.

Day	Images		Percentage Used
	Used	Missed	
1	24	0	100
Total:	24	0	100

THRESHOLD TEMPERATURE (Celsius).

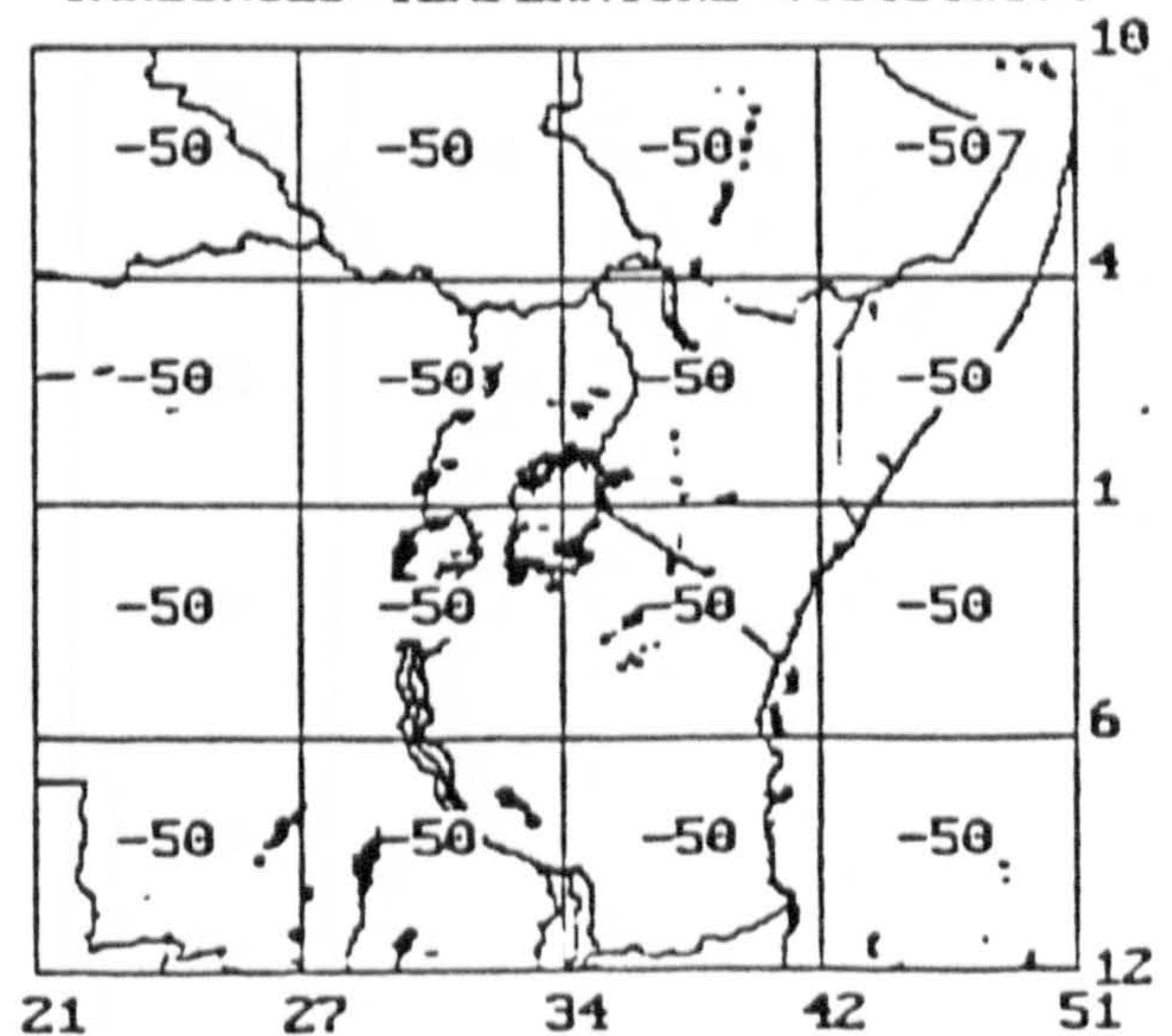
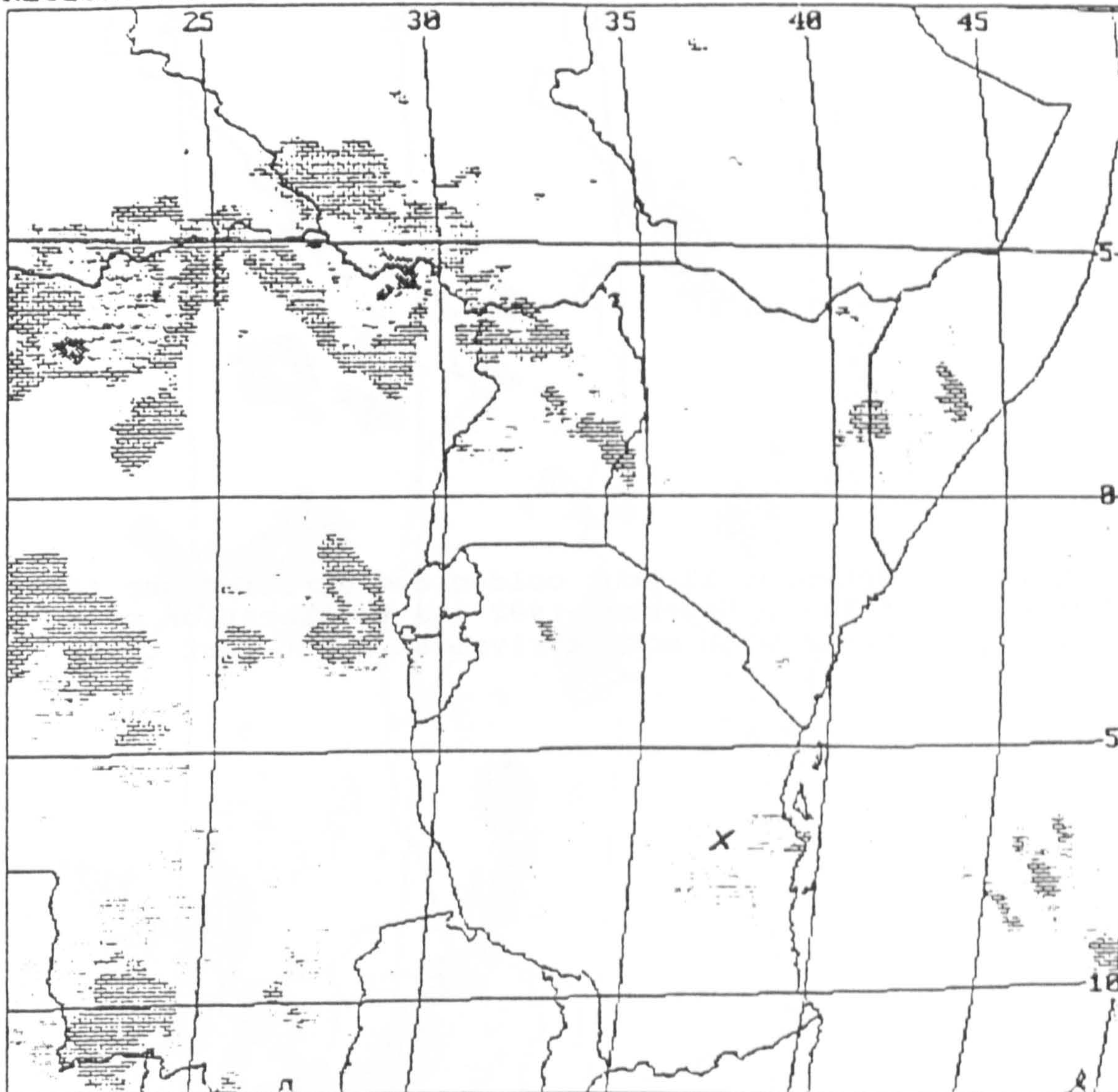


Figure 32. Meteosat 12-hour cold-cloud duration map for the night of 10-11 November 1992 and the location of a primary outbreak with moth arrival at about that time.

HALF DAY COLD CLOUD DURATION MAP.

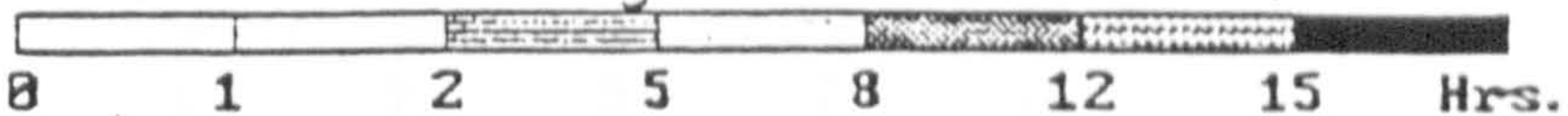
REGION: EASTERN AFRICA PRINTED AT: NRI



Start time: 15:00 10/11/1992

Filename: UGCHFABF.CCD

COMMENTS: NB. E-C Tanzania minstorms



x Outbreak location

IMAGE USAGE INFORMATION.

Day	Images		Percentage Used
	Used	Missed	
1	24	0	100
Total:	24	0	100

THRESHOLD TEMPERATURE (Celsius).

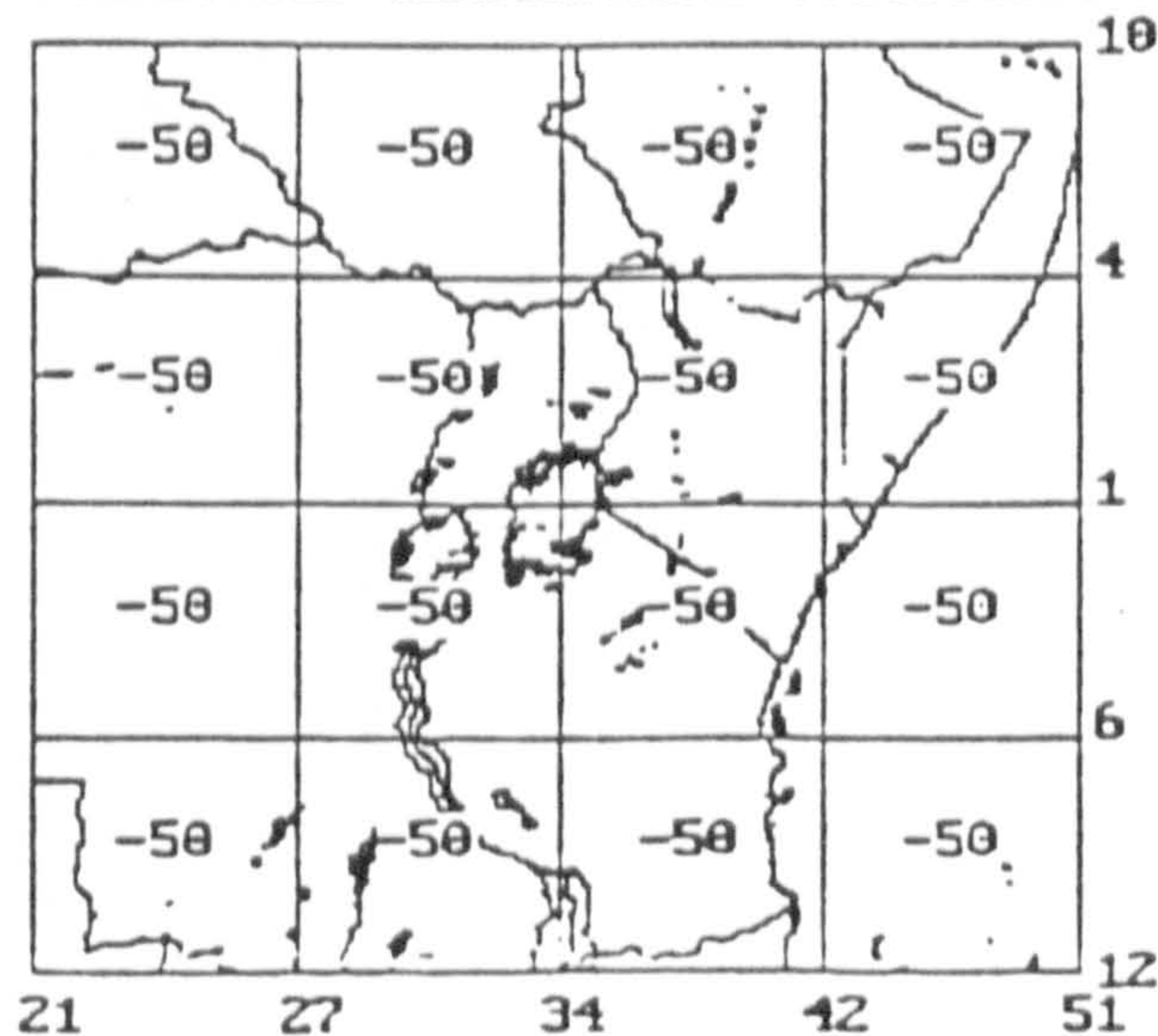
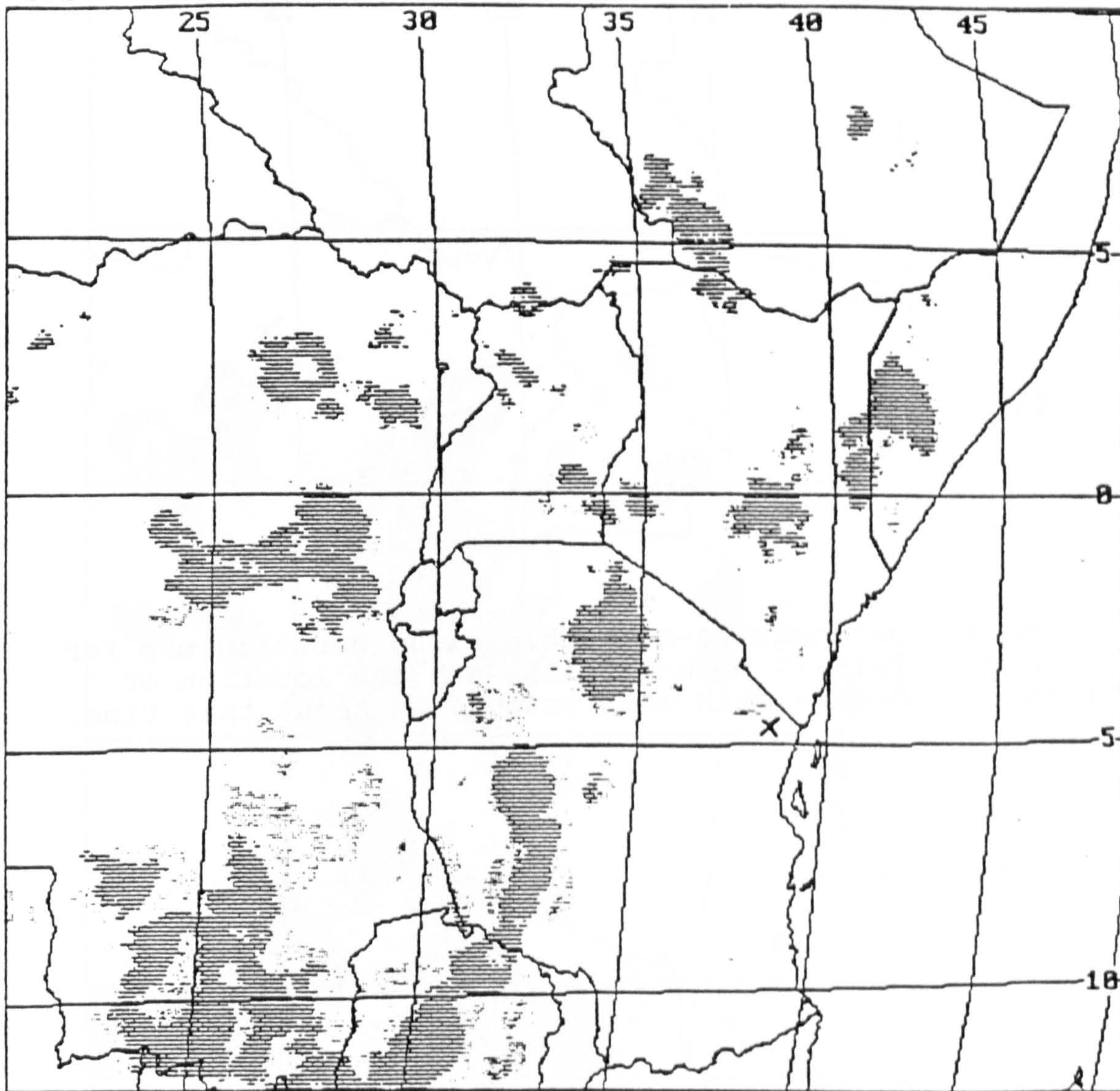


Figure 33. Meteosat 12-hour cold-cloud duration map for the night of 14-15 November 1992 and the location of a primary outbreak with moth arrival at about that time.

HALF DAY COLD CLOUD DURATION MAP.

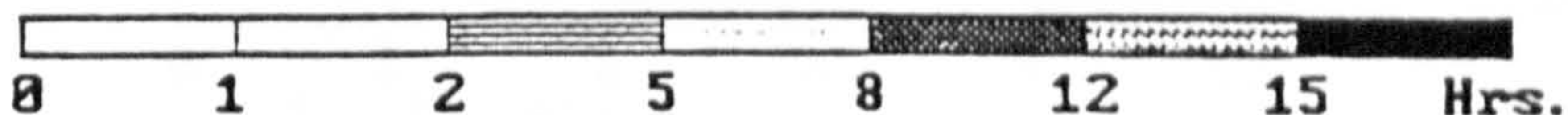
REGION: EASTERN AFRICA. PRINTED AT: NRI.



Start time: 15:00 14/11/1992

Filename: UGCHFEBF.CCD

COMMENTS:



x Outbreak location

IMAGE USAGE INFORMATION.

Day	Images		Percentage Used
	Used	Missed	
1	24	0	100
Total:	24	0	100

THRESHOLD TEMPERATURE (Celsius).

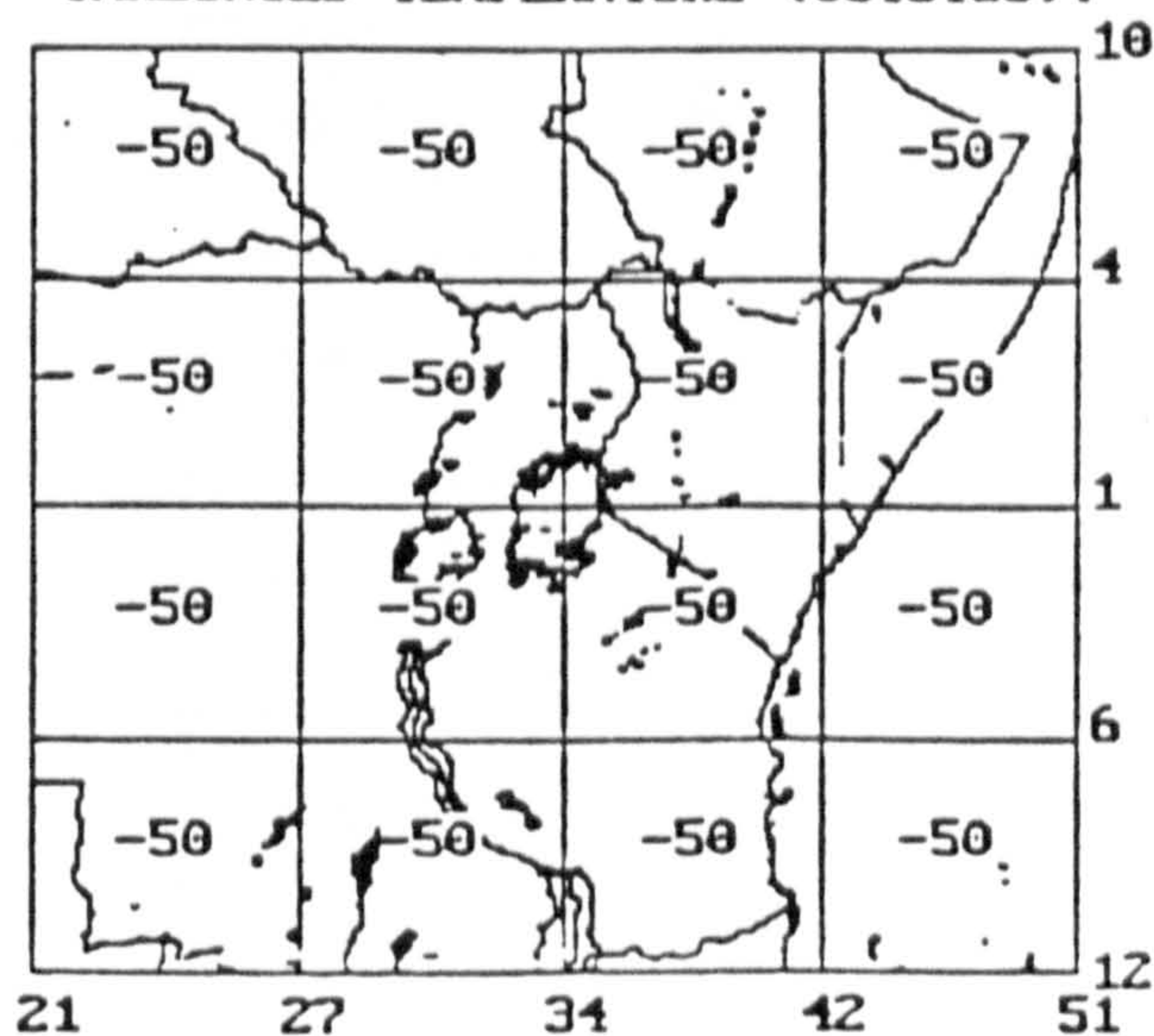
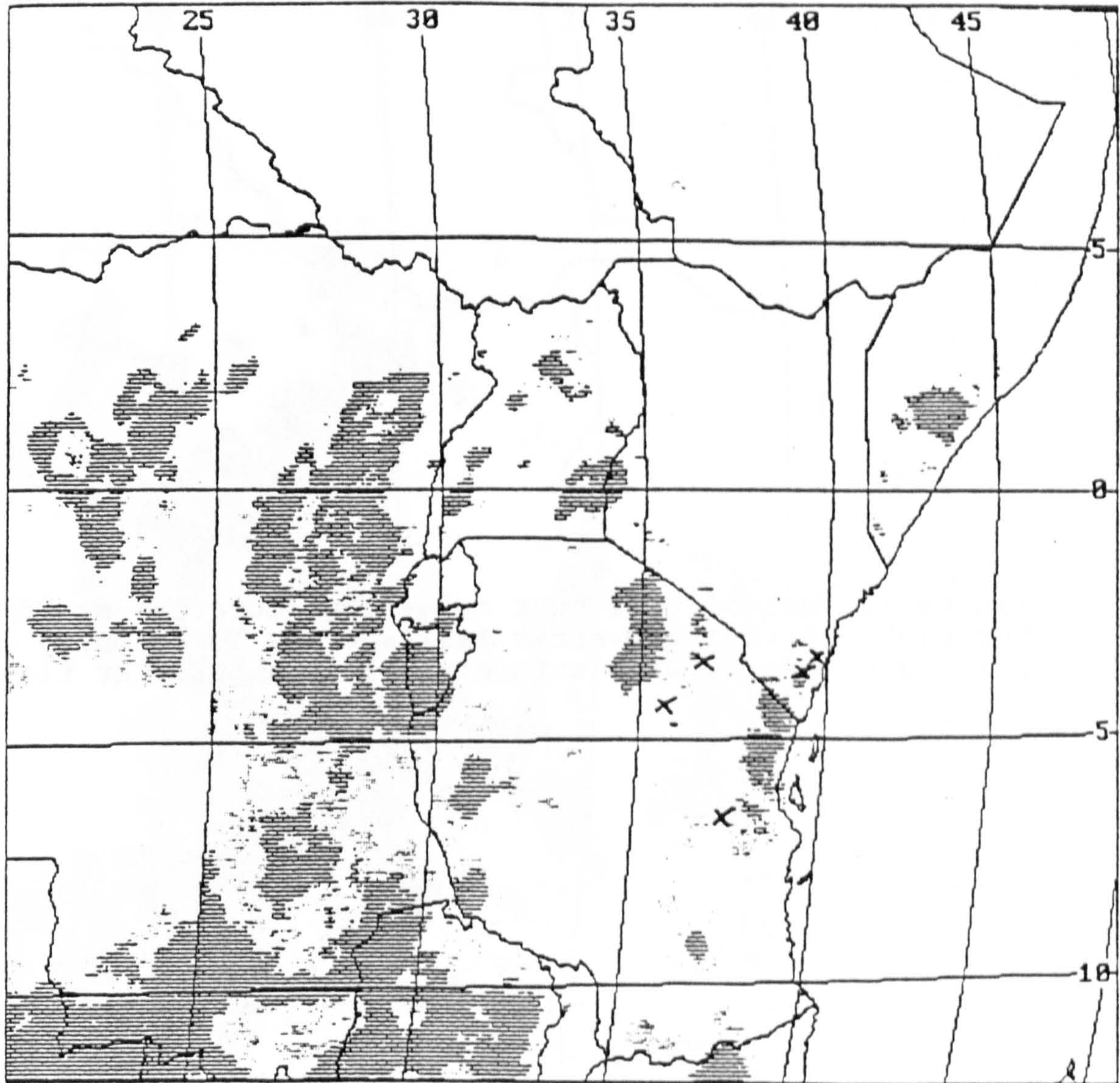


Figure 34. Meteosat 12-hour cold-cloud duration map for the night of 16-17 November 1992 and the location of primary outbreaks with moth arrival at about that time.

HALF DAY COLD CLOUD DURATION MAP.

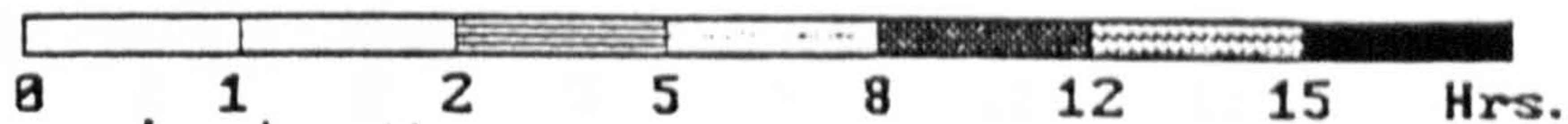
REGION: EASTERN AFRICA. PRINTED AT: NRI.



Start time: 15:00 16/11/1992

Filename: UGCHFGBF.CCD

COMMENTS:



X Outbreak locations

IMAGE USAGE INFORMATION.

Day	Images		Percentage Used
	Used	Missed	
1	24	0	100
Total:	24	0	100

THRESHOLD TEMPERATURE (Celsius).

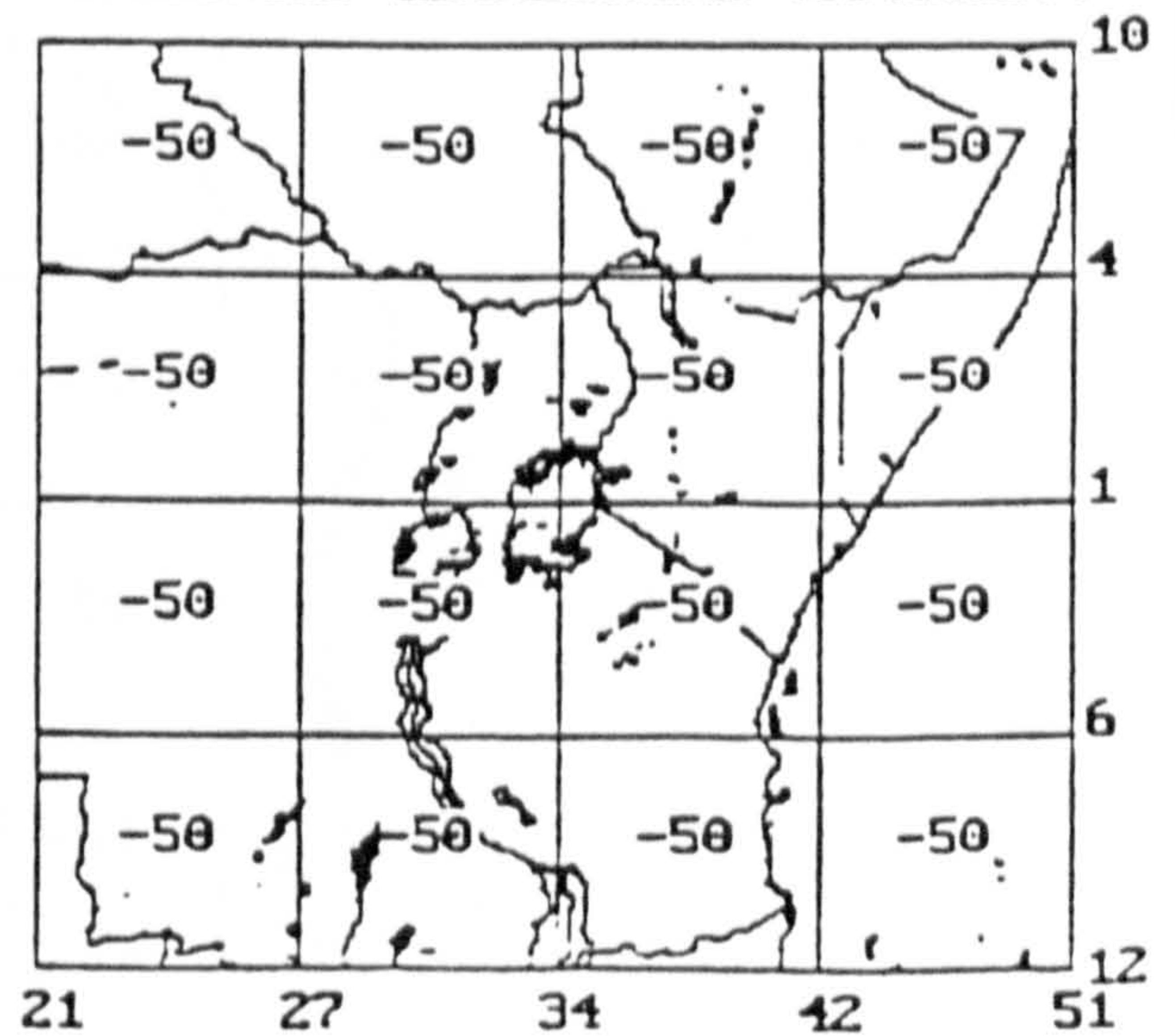
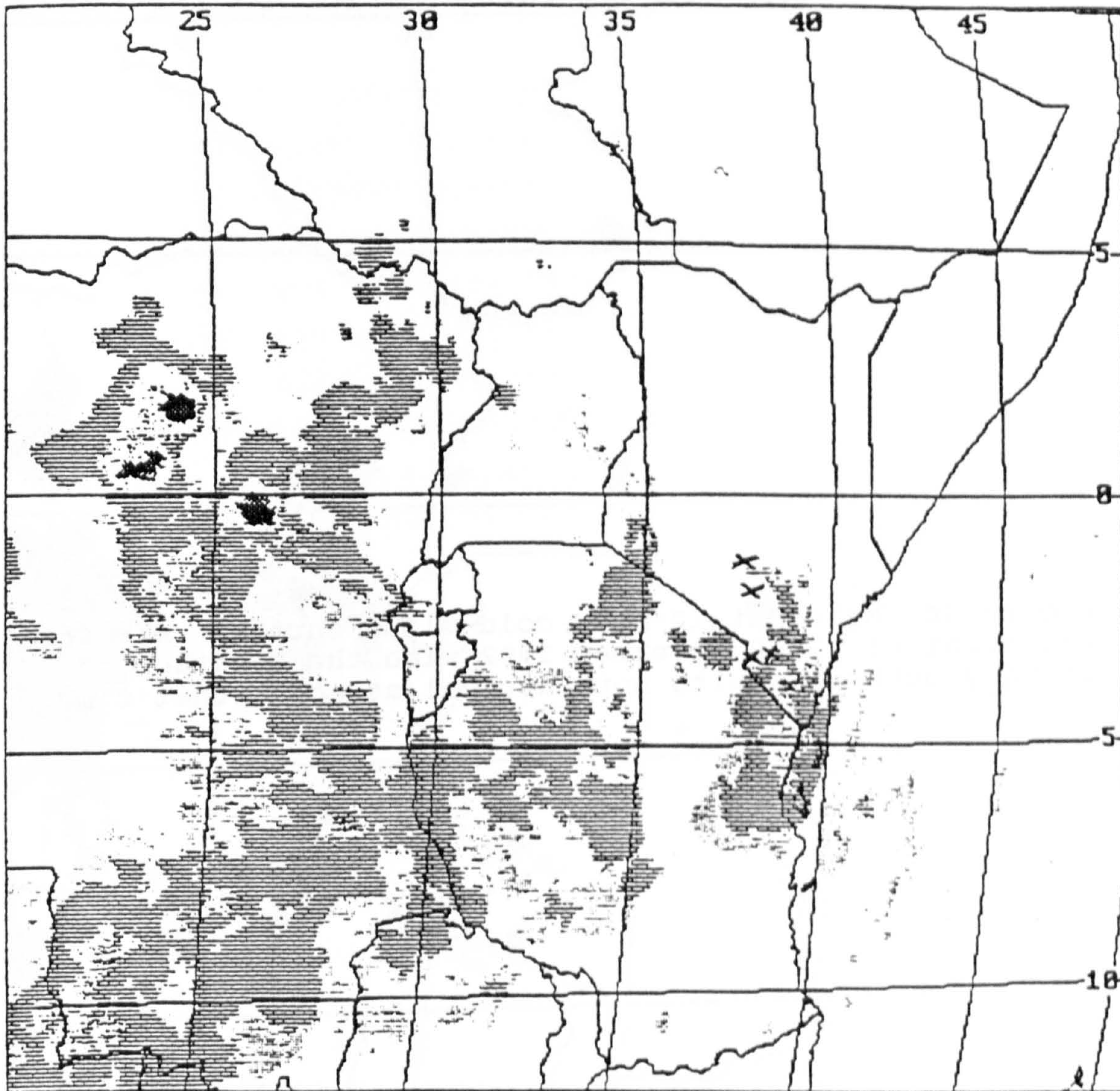


Figure 35. Meteosat 12-hour cold-cloud duration map for the night of 18-19 November 1992 and the location of primary outbreaks with moth arrival at about that time.

HALF DAY COLD CLOUD DURATION MAP.

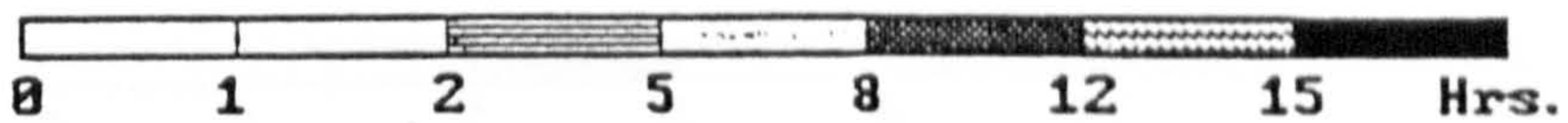
REGION: EASTERN AFRICA. PRINTED AT: NRI.



Start time: 15:00 18/11/1992

Filename: UGCHFIBF.CCD

COMMENTS:



x Outbreak locations

IMAGE USAGE INFORMATION.

Day	Images		Percentage
	Used	Missed	Used
1	24	0	100
Total:	24	0	100

THRESHOLD TEMPERATURE (Celsius).

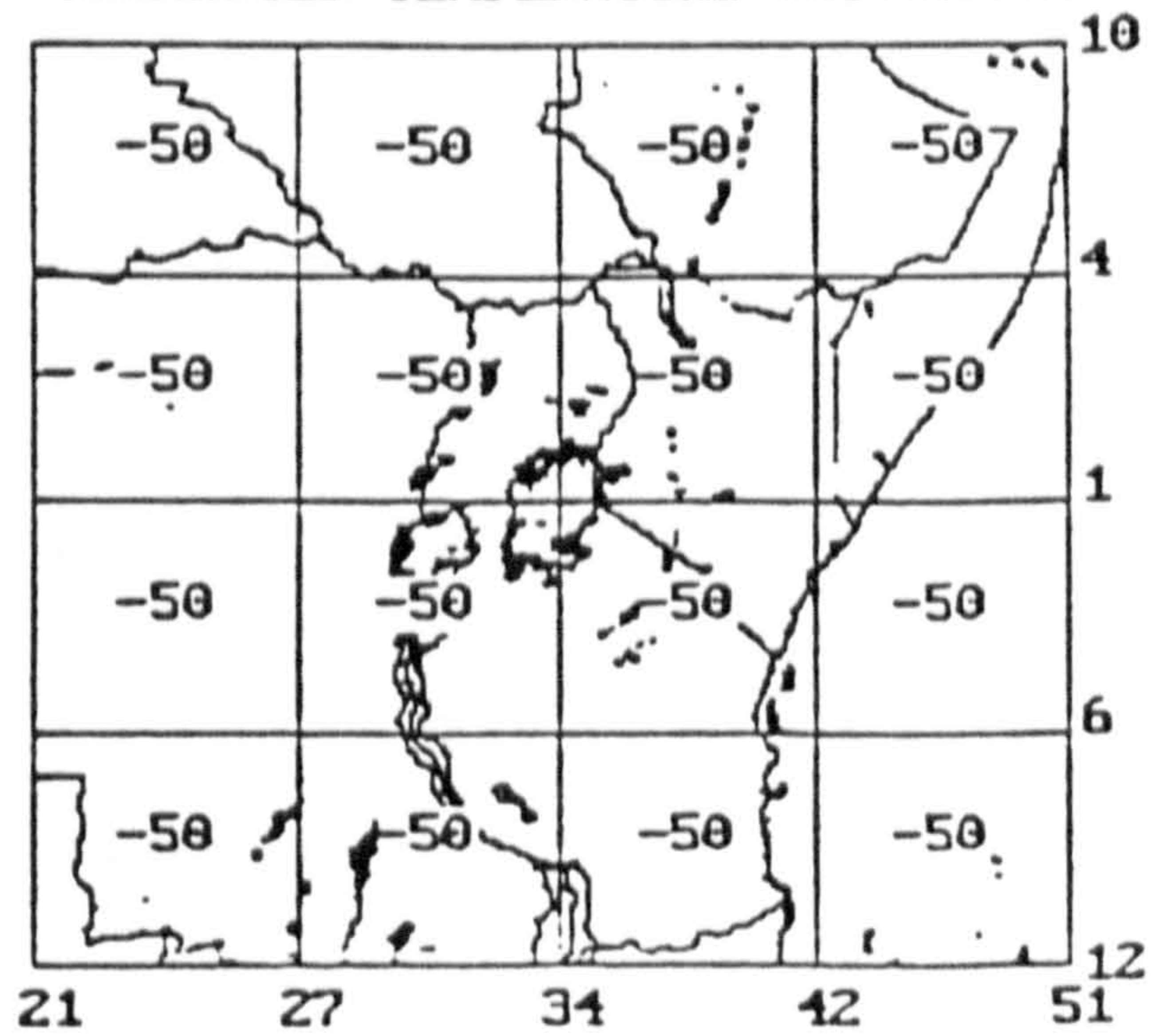
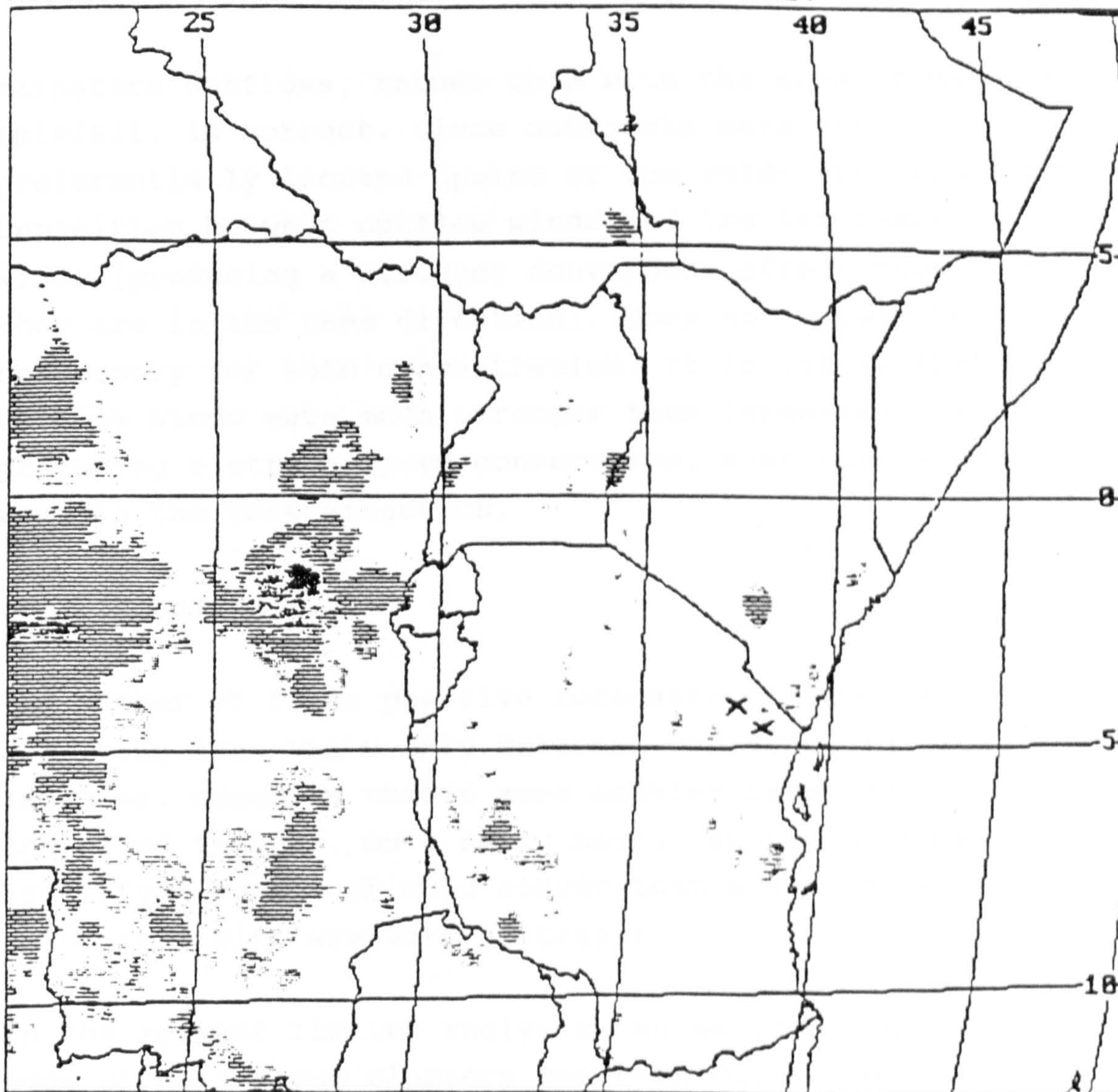


Figure 36. Meteosat 12-hour cold-cloud duration map for the night of 27-28 November 1992 with the location of primary outbreaks with moth arrival at about that time.

HALF DAY COLD CLOUD DURATION MAP.

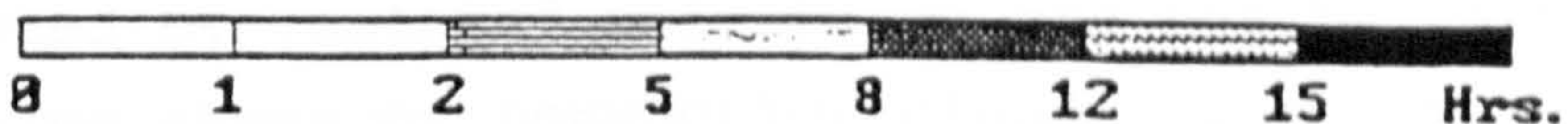
REGION: EASTERN AFRICA. PRINTED AT: NRI.



Start time: 15:00 27/11/1992

Filename: UGCHFRBF.CCD

COMMENTS:

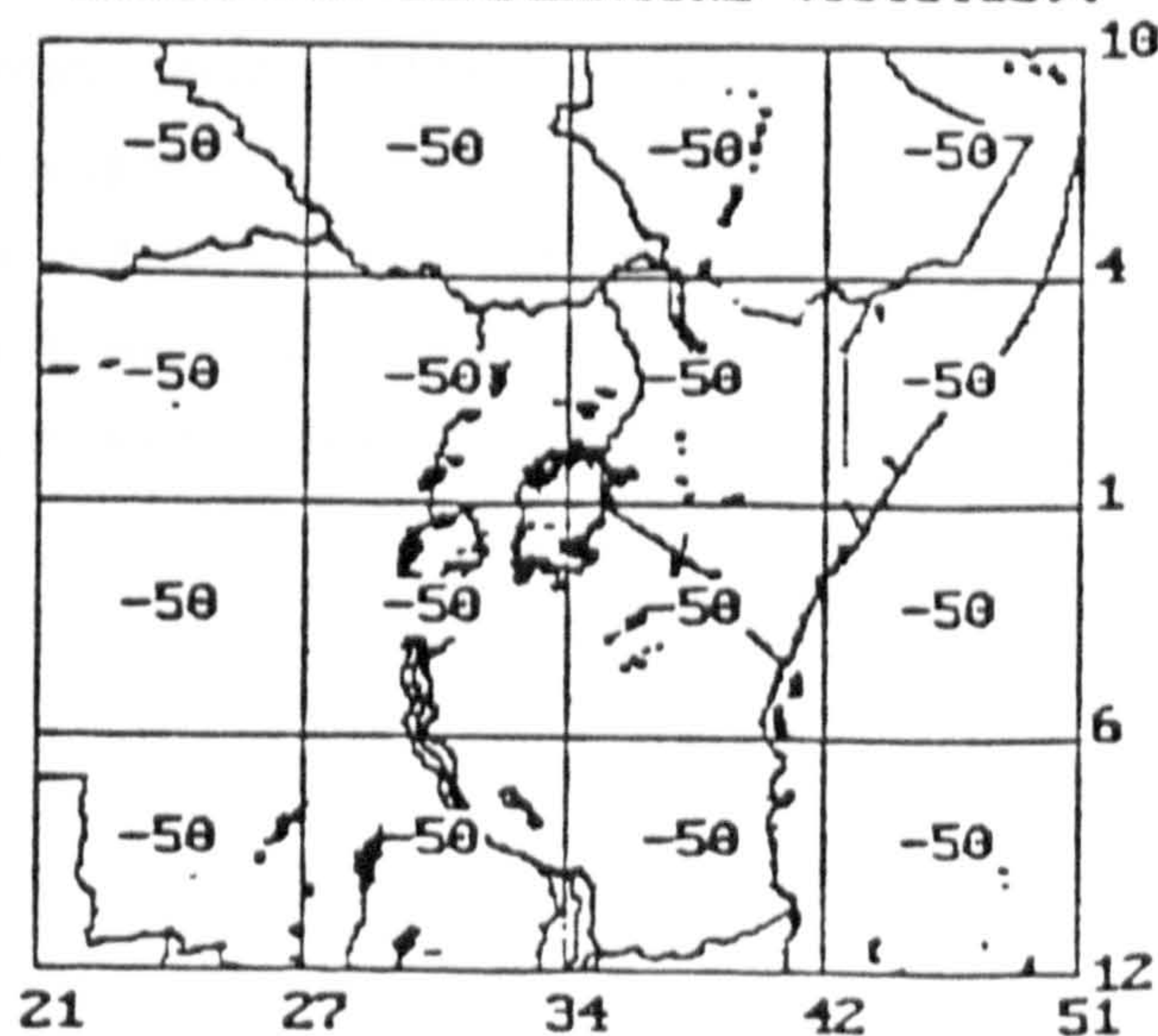


x Outbreak locations

IMAGE USAGE INFORMATION.

Day	Images		Percentage
	Used	Missed	Used
1	24	0	100
Total:	24	0	100

THRESHOLD TEMPERATURE (Celsius).



rainstorm outflows, rather than with the area of maximum rainfall, is correct. Since outbreaks were not preferentially located upwind of the cold-cloud clusters, opposition between outflow winds and the large-scale winds (producing a stronger convergent effect than when they are in the same direction), does not appear to be necessary for moth concentration. It is likely that outflow winds were much stronger than large-scale winds producing a strong speed-convergence, even when winds were in the same direction.

(d) Discussion

The number of false positive forecasts of outbreaks resulting from the weekly Meteosat-derived cold-cloud analyses, suggests that a more sophisticated analysis of the cloud imagery, on a daily basis, should be able to identify a subset of cold clouds that are most frequently associated with armyworm outbreaks.

In the present limited analysis, an association with the edge of cold-cloud clusters has been found. This is consistent with armyworm moths being preferentially concentrated by isolated rainstorms and not by rainstorms within large areas of convective clouds, where winds are likely to be more variable and most individual storm outflows less strong. Thus although on 16 and 18 November there were large areas of cold cloud consisting of many individual storms, each probably causing downdraughts, outbreak locations were all on the edge of the cold cloud. There were also no prolonged periods of frequent rainstorms, such as occurred in the very low armyworm seasons.

Forecasts should, therefore, be improved by the following assumptions:

i) moth concentration leading to outbreaks is most likely to occur associated with the first rainstorms after a dry period.

ii) Moth concentration occurs mainly at the edge of cold cloud clusters identified from individual-night cold-cloud-duration images.

In comparison with NOAA vegetation index imagery, monitoring rainstorms from Meteosat has the advantage that, if the conclusions about moth concentration are correct, rainstorm data will give several days notice of a likely outbreak, even before vegetation has started to green, and will also pick out rainstorms most likely to be associated with armyworm outbreaks. Vegetation index data, on the other hand, identifies all areas where rainfall has been sufficient for grasses to sprout, which are likely to be much larger than outbreak areas. Because there is a delay between rainfall and vegetation greening, armyworms that are present are likely to be hatching by the time the vegetation index increases significantly.

Further work is needed to confirm that rainstorms identified from Meteosat cold-cloud imagery are significantly associated with African armyworm outbreaks. While there is some uncertainty as to the accuracy of both Meteosat cold-cloud and NOAA NDVI as methods of forecasting outbreaks, a combination of both methods may be found to give the best results.

CHAPTER 8. GENERAL DISCUSSION AND CONCLUSIONS

The distinction between primary and secondary outbreaks of *Spodoptera exempta* has been shown to be a useful one, at least for eastern Africa. The distribution of these outbreaks in time and space supports the hypotheses that armyworm outbreaks at the beginning of the season are derived from low-density populations (H_1) and mostly occur in identifiable 'primary outbreak areas' (H_2) but that later outbreaks are mostly secondary (H_3). When late primary outbreaks do occur, usually after a dry period, they can be economically very important, as in 1983-84. Evidence has been presented which supports the association of individual outbreaks with rainstorms, particularly, from satellite data, with the edges of storms where low-level outflows occur (H_5). The inverse association between armyworm season severity and early season rainfall has been supported, mainly by the association of very low armyworm seasons with heavy prolonged short rains rainfall (H_6).

The concept of 'critical' outbreaks, as used in this work, is very much linked to the amount of economic damage caused by subsequent crop loss or pasture damage and is the basis of strategic armyworm control methods. This has been mentioned here only briefly, but Cheke & Tucker (1995) have built on the economic assessments of Rose *et al* (1988) and Scott (1991), and the trajectory analyses included in the present work, to evaluate the potential economic returns of the strategic control approach to managing African armyworm outbreaks. They concluded that strategic control operations were justified in the main primary outbreak areas (as shown in Figure 8) which acted as sources and were also frequently important crop growing themselves. This is also true, for example, in southwestern Kenya where crops values are high and where more than one generation of outbreaks

frequently occur in the same broad area, and in southern Morogoro region which, while not an important crop area itself (and which includes the Selous Game Reserve), is an important potential source area.

Moth migrations of several hundred kilometres and up to 950 km have been shown to occur. Wilson & Gatehouse (1993) and (in preparation) have developed a model relating moth migration (measured by the pre-reproductive period) to moth genetics and environmental conditions, which concludes that migratory potential decreases as habitats become more stable later in the season.

'Migratory potential' is an indication of the probability of migratory *behaviour* taking place. This is not necessarily the same as migration with ecological consequences, such as displacements of populations over many kilometres, as discussed by Gatehouse (1987). In the present study, therefore, the long moth migrations found from eastern Kenya to Ethiopia in April and May, while demonstrating that high migratory potential does persist late in the armyworm season, does not, necessarily, invalidate a trend towards lower migratory potential in the population as a whole. Also, from an ecological perspective, long-distance migrations north from Kenya to Ethiopia occurred in years with severe January-March dry seasons (e.g. 1983-84). Together with the findings of Haggis (in press) relating armyworm seasonal severity not only to early season rains but also the previous long rains, this can be incorporated into a generalised, qualitative model of *Spodoptera exempta* population dynamics during the season. This overview represents a significant increase in our understanding of African armyworm. It can be used to improve forecasting and also identifies relationships which might be quantified by further work to provide a more sophisticated 'expert system' model. This in turn could be incorporated into

the 'Wormbase' database and expert system developed by Day (1991).

Generalised progress of *Spodoptera exempta* during the season in eastern Africa.

A. Start of the season

1. The rate of increase of low-density populations in off-season survival areas is dependent on the nutritional value of grasses. This is increased by a prolonged dry period and therefore is likely to be higher following poor long rains (March-May) and when short rains are delayed (October-December).

2. The presence of long-distance migrants in the population results in migration from coast to inland hills.

3. Flying moths are concentrated by isolated early season rainstorms occurring on hills of east-central Kenya and Tanzania (October-December).

4. First primary outbreaks are formed (October-December). Gregarisation is associated with the first noticeable crop damage by armyworms and a subsequent further increase in proportion of potential migrants.

5. When early rains are very widespread over space and time, outbreaks are likely to be very dispersed or may not form at all, resulting in a dispersed low-density population.

6. When subsequent rains are heavy and persistent armyworm survival is reduced.

7. Moths emerging from primary outbreaks migrate downwind.

8. A proportion of migrating moths caught up in downdraughts of widely scattered rainstorms, resulting in reconcentration and the formation of the first secondary outbreaks (November-January).

B. Mid-late armyworm season

9. First secondary outbreaks develop during and immediately after the short rains (November-January). There may be a reduction in proportion of moths with migratory potential.

10. Occasionally, further primary outbreaks are formed from low-density populations remaining near the coast.

11. Further generations of secondary outbreaks follow downwind migration and reconcentration. During the January-early-March dry season in Kenya and northern Tanzania, rainstorms are infrequent, so there are usually few opportunities for outbreak formation. Those that do form, however, are often large.

12. At the beginning of the long-rains (late March-early April), outbreaks associated with isolated rainstorms following dry weather are likely to give moths with high migratory potential.

13. Later in the long-rains (mid-April-May), widespread rains lead to both widespread outbreaks and possibly a dispersed low-density population. The proportion of moths with high migratory potential is likely to decrease.

14. In years with severe January-March dry seasons, late primary outbreaks may appear in March-April, especially

on the coast. Primary outbreaks may also occur in southern Ethiopia on first rains there. Such primary outbreaks are likely to contain a proportion of moths with high migratory potential.

15. The onset of strong southerly winds in eastern Kenya and Tanzania in April onwards provide the means for long-distance migration northwards towards Ethiopia.

16. Secondary outbreaks are formed in northern Kenya and southern Ethiopia.

C. End of armyworm season and off-season (Kenya-Tanzania)

17. In the June-September rainy season in Ethiopia, there are usually several generations of secondary outbreaks. The proportion of long-distance migrants probably decreases over time.

18. In the June-September dry season in Kenya/Tanzania, any remaining outbreaks pupate in June/July and moths disperse to give rise to low-density populations or die.

19. During this period, low-density populations survive in favoured areas, mostly on the coast. Numbers of moths with migratory potential is low.

This work also aimed to describe techniques that can be used to improve armyworm forecasting especially those involving environmental monitoring from satellites. The use of Meteosat imagery to identify rainstorms, that may be associated with armyworm moth concentration and subsequent outbreak formation, especially at the beginning of the armyworm season, has been described. The use of NOAA satellite imagery for monitoring vegetation has been considered in detail by Robinson (1991). His results together with those of Davenport & Nicholson

(1993) indicate that NDVI may be best used to monitor large-scale differences between seasons in areas with mean annual rainfall of <1000mm rather than to forecast individual outbreaks. Potentially, satellite-derived data could be included in computerised forecasting systems such as that provided by 'Wormbase' (Day 1991). However a major problem is the massive amount of data generated by satellites, often in a form not immediately compatible with simple distribution maps of armyworm outbreaks, or even conventional weather or crop data. The best procedure would seem to be to pre-process as much of the satellite data as possible so as to output only the minimum, most significant data. This is already being done in practice with Meteosat data, where nightly cold-cloud data are summarised for the forecaster into weekly occurrences of cold cloud on a degree-square basis. This, however, gives only broad areas (of 100 x 100 km) where outbreaks might occur and more precision (to the nearest 10 km) should be possible using Meteosat data.

Software has been developed, at NRI, to incorporate Meteosat imagery into the IDRISI geographical information system. The aim of incorporating both remote-sensing and surface data into a GIS where all variables can be compared on a spatial basis has also been pursued by A. Harvey (personal communication).

Finally it must be remembered that the aim of armyworm forecasting is to help farmers, many of whom live at or near subsistence level, to reduce crop losses due to the pest. Sophisticated computerised forecasting systems are only justified if they are sustainable in the countries affected and if they do not absorb funds which would be more efficiently spent on low-technology answers to the problem. The findings of the present work are applicable,

whatever the means employed, providing the infrastructure for reporting and analysing armyworm data, and disseminating the results to extension workers and others who can implement control measures, is maintained.

Glossary

- Armyworm phase Refers to the morphological variation in *Spodoptera exempta* between gregaria and solitaria extreme forms.
- Backtracks Trajectories drawn backwards from armyworm outbreaks to estimate moth sources.
- Critical outbreak An outbreak leading to large numbers of subsequent outbreaks, usually over several generations.
- Degree square An area on a map of one degree of latitude by one degree of longitude.
- Development table A table showing the mean duration of each stage of the armyworm life-cycle, especially of larval instars, in relation to temperature or altitude.
- Forward tracks Trajectories drawn forward from armyworm outbreaks to estimate the possible destination(s) of departing moths.
- Gregaria The armyworm phase distinguished by the black colouring and high activity of the caterpillars, but also by other morphological, biochemical, physiological and behavioural characteristics.
- LT (local time) Local time as distinct from Zulu (or GMT)
- Moth arrival The most likely date(s) on which moths arrive at a locality and are concentrated prior to mating and oviposition, leading to an armyworm outbreak.

Outbreak	Armyworm caterpillars at high density, usually over a well-defined area.
Primary	An outbreak originating from moths coming outbreak from low-density populations.
Secondary	An outbreak originating from moths coming outbreak from a previous outbreak.
Solitaria	The armyworm phase distinguished particularly by green or brown colouring and low activity of the caterpillars but also by other morphological, bio-chemical, physiological and behavioural characteristics.
Squall-line	A curvi-linear feature over tens of kilometres, where an abrupt change in wind direction and increase in wind speed accompanies the outflow from a convective rainstorm.
Synoptic-scale convergence	A zone where winds converge on a scale of hundreds or thousands of kilometres, caused by large-scale pressure patterns, usually pressure 'troughs'. It is often associated with rainfall.
Trajectory	A line drawn on a map parallel to the windflow; (for periods from several hours to several days) of a length determined by the windspeed, and used to estimate the displacements of air parcels and hence the migration of windborne moths.
Windfield	An area of winds differing from the disturbance prevailing winds, usually with

a well-defined structure and lasting from one to several days.

Wind rotor An area of overturning winds caused by the barrier effect of topography, usually over an area of tens of kilometres.

Wind streamlines Continuous lines on a windfield map drawn parallel to the wind direction and indicating structures in the windfield, such as windfield disturbances and synoptic-scale convergence. Trajectories follow wind streamlines for the appropriate time and location.

REFERENCES

- ACHTEMEIER, G.L. (1991) Observations of turbulent boundary-layer interaction with a thunderstorm outflow - a possible wake region energy source. *Boundary layer Meteorology* 55: 309-324.
- ANDERSON, D.L.T. (1976) The low level jet as a western boundary current. *Monthly Weather Review* 104, 907-921.
- ARKIN, D.A. & MEISNER, B.N. (1987) The relationship between large-scale convective rainfall and cold cloud over the western hemisphere during 1982-84. *Monthly Weather Review* 115, 51-74.
- BAKER, R.R. (1978) *The evolutionary ecology of animal migration*. Hodder & Stoughton 1011pp.
- BAKER, R.R. & MATHER J G (1982) Magnetic compass sense in the large yellow underwing moth, *Noctua pronuba* L. *Animal Behaviour* 30: 543-548.
- BARRETT, E.C. (1974) *Climatology from satellites*. Methuen & Co. Ltd 418pp.
- BARRING, L. (1987) Spatial patterns of daily rainfall in central Kenya: Applications of principle component analysis, common factor analysis and spatial correlation. *Journal of Climatology* 7: 267-289.
- BARRY, R.G. & PERRY, A.H. (1973) *Synoptic Climatology. Methods and Applications*. Methuen & Co. Ltd London. 555pp.
- BEGON, M. & MORTIMER, M. (1986) *Population ecology - A unified study of animals and plants* (2nd edition). Blackwell Scientific Publications, Oxford. 220pp.
- BOWDEN, J. (1973) The influence of moonlight on catches of insects in light-traps in Africa. Part 1. The moon and moonlight. *Bulletin of Entomological Research* 63: 113-128.
- BOWDEN, J. (1982) An analysis of factors affecting catches of insects in light-traps. *Bulletin of Entomological Research* 72: 535-556.

- BOWDEN, J. and CHURCH, B.M. (1973) The influence of moonlight on catches of insects in light-traps in Africa. Part 2. The effect of moon phase on light-trap catches. *Bulletin of Entomological Research* 63: 129-142.
- BROWN, E.S. (1962) The African armyworm *Spodoptera exempta* (Wlk) (Lepidoptera: Noctuidae). A Review of the Literature Commonwealth Agricultural Bureau (reprinted 1972).
- BROWN, E.S. (1965) Biological and ecological aspects of research on the African armyworm. In The application of biological research to the development of East Africa (Abstracts of papers). *Journal of Applied Ecology* 2: 405.
- BROWN, E.S. & MOHAMED, A.K. (1972) The relation between simulated armyworm damage and crop-loss in maize and sorghum. *East African Agricultural and Forestry Journal* 37: 237-257.
- BROWN, E.S., BETTS, E. & RAINEY, R. C. (1969) Seasonal changes in distribution of the African armyworm, *Spodoptera exempta* (Wlk) (Lepidoptera: Noctuidae), with special references to eastern Africa. *Bulletin of Entomological Research* 58: 661-728.
- BROWN, E.S. and SWAINE, G. (1966) New evidence on the migration of moths in African Armyworm *Spodoptera exempta* (Wlk) (Lepidoptera Noctuidae). *Bulletin of Entomological Research* 56: 671-684.
- BRADFORD UNIVERSITY RESEARCH LTD (1991) *BURL Meteosat Primary, Relayed DCP and WEFAX-Secondary Data Receiver System Autosat Software Users Manual. Version 3.1.*
- BUNTIN, G.D., PEDIGO, L.P. & SHOWERS, W.B. (1990) Temporal occurrence of the variegated cutworm Lepidoptera Noctuidae adults in Iowa USA with evidence for migration. *Environmental Entomology* 19: 603-608.

- CAMPION, D.G., BETTANY, B.W., MCGINNIGLE, J.B. & TAYLOR, L.R. (1977) The distribution and migration of *Spodoptera littoralis* (Boisd.) (Lepidoptera: Noctuidae) in relation to meteorology on Cyprus, interpreted from maps of pheromone trap samples. *Bulletin of Entomological Research* 67: 501-522.
- CAMPION, D.G., ODIYO, P.O., MUSHI, A.M., HALL, D.R., LESTER, R. & NESBITT, B.F. (1976) Field tests with the synthetic sex pheromone of the African armyworm, *Spodoptera exempta* (Wlk). *Miscellaneous Report No. 25*, Centre for Overseas Pest Research, London.
- CHAGGAR, T.S. (1977) Geographical distribution of monthly and annual mean frequency of thunderstorm days over eastern Africa. *East African Meteorological Department Technical Memorandum No. 26*.
- CHEKE, R.A. & TUCKER M.R. (1995). An evaluation of potential economic returns from the strategic control approach to the management of African armyworm *Spodoptera exempta* (Lepidoptera: Noctuidae) populations in eastern Africa. *Crop Protection* 14: 91-103.
- CHEN, R.L., BAO, X.Z., DRAKE, V.A., FARROW, R.A., WANG, S.Y., SUN, Y.J. & ZHAI, B.P. (1989) Radar observations of the spring migration into north-eastern China of the oriental armyworm, *Mythimna separata* and other insects. *Ecological Entomology* 14: 149-162.
- COAKER, T.H. (1959) Investigation on *Heliothis armigera* (Hb) in Uganda. *Bulletin of Entomological Research* 50: 487-506.
- COLVIN, J. & GATEHOUSE, A.G. (1993) The reproductive-flight syndrome and the inheritance of tethered-flight activity in the cotton bollworm moth, *Heliothis armigera*. *Physiological Entomology* 18: 16-22.

- DAVENPORT, M.L. & NICHOLSON, S.E. (1993) On the relation between rainfall and the Normalized Difference Vegetation Index for diverse vegetation types in East Africa. *International Journal of Remote Sensing* 14: 2369-2389.
- DAVIES, T.D., VINCENT, C.E., & BERESFORD, A.K.C. (1985) July-August rainfall in west-central Kenya. *Journal of Climatology* 5: 17-33.
- DAY, R. (1991) 'Wormbase' armyworm database and forecasting system user manual. Imperial College (Silwood)/NRI.
- DEN BOER, M.H. (1978) Isoenzymes and migration in the African armyworm (*Spodoptera exempta*) (Lepidoptera: Noctuidae). *Journal of Zoology, London*. 185: 539-553.
- DINGLE, H (1986) Evolution and genetics of insect migration. pp 11-26 In: DANTHANARAYANA, W. [Ed] *Insect flight-dispersal and migration*. Based on a symposium at the 17th International Congress of Entomology, Hamburg 1984, Springer-Verlag, Berlin, 289pp.
- DRAKE, V.A. (1982) Insects in the sea-breeze front at Canberra: A radar study. *Weather* 37: 134-143.
- DRAKE, V.A. (1984) The vertical distribution of macro insects migrating in the nocturnal boundary layer, a radar study. *Boundary layer Meteorology* 28: 353-374.
- DRAKE, V.A. (1985) Solitary wave disturbances of the nocturnal boundary layer revealed by radar observations of migrating insects. *Boundary layer Meteorology* 31: 269-286.
- DRAKE, V.A. and FARROW, R.A. (1985) A radar and aerial-trapping study of an early spring migration of moths (Lepidoptera) in inland New South Wales. *Australian Journal of Ecology* 10: 223-235.

- DRAKE, V.A. & FARROW, R.A. (1988) The influence of atmospheric structure and motions on insect migration. *Annual Review of Entomology* 33: 183-210.
- EAST AFRICAN METEOROLOGICAL DEPARTMENT (1975). *Climatological statistics for east Africa. Part III. Tanzania.*
- FARMER, G. (1988) Seasonal forecasting of the Kenya coast short rains, 1901-84. *Journal of Climatology* 8: 489-497.
- FARROW, R.A. (1990) Flight and migration in Acridoids pp 227-314 In CHAPMAN, R.F. & JOEM, A. [Eds] *Biology of grasshoppers.* J Wiley & Sons.
- FARROW, R.A. & MCDONALD, G. (1987) Migration strategies and outbreaks of noctuid pests in Australia. *Insect Science and its Applications* 8: 531-542.
- FAURE, J.C. (1943) Phase variation in the armyworm *Laphygma exempta* (Walker). Department of Agriculture and Forestry. *South African Science Bulletin* No.234.
- FINDLATER, J. (1966) Cross-equatorial jet streams at low level over Kenya. *Meteorological Magazine* 95: 353-364.
- FINDLATER, J. (1967) Cross-equatorial jet streams at low level over Kenya. Part 2 Some further evidence. *Meteorological Magazine* 96: 53-56.
- FINDLATER, J. (1969) A major low-level current near the Indian Ocean during northern summer. *Quarterly Journal of the Royal Meteorological Society* 95: 362-380.
- FLOHN, H. (1965) Contributions to the synoptic climatology of northeast Africa. *WMO Technical Notes* 69: 236-244.
- GARLAND, A C (1985) Use of Meteosat in the analysis of African armyworm outbreaks in East Africa. *PhD thesis, University of Bristol, 297pp.*

- GATEHOUSE, A.G. (1986) Migration in the African armyworm *Spodoptera exempta*: Genetic determination of migratory capacity and a new synthesis. In: *Insect Flight: Dispersal and Migration*. Ed. Danthanarayana, W. Springer Verlag, 128-144.
- GATEHOUSE, A. G. (1987a) Migration and low population density in armyworm (Lepidoptera: Noctuidae) Life histories. *Insect Science and its Application* 8: 573-580.
- GATEHOUSE, A.G. (1987b) Migration and dispersal of tropical noctuid moths: Summing up the symposium. *Insect Science and its Applications* 8: 605-608.
- GATEHOUSE, A G (1987c) Migration: A behavioural process with ecological consequences? *Antenna*
- GIBO, D.L. (1986) Flight strategies of migrating butterflies (*Danaus plexippus* L.) in southern Ontario. pp 172-184 In: *Insect flight -Dispersal and Migration*, Ed. DANTHANARAYANA, W. Springer-Verlag, Berlin.
- GRAY, W.M. (1979) Hurricanes: their formation, structure and likely role in the tropical circulation. pp 155-218 In SHAW, D.B. [Ed] *Meteorology over the Tropical Oceans*. Royal Meteorological Society Bracknell, UK.
- HACKETT, D.S. & GATEHOUSE, A.G. (1982) Diapause in *Heliothis armigera* (Hubner) and *Heliothis fletcheri* (Hardwick) (Lepidoptera Noctuidae) in the Sudan Gezira. *Bulletin of Entomological Research* 72: 409-422.
- HAGGIS, M.J. (1981) Spatial and temporal changes in distribution of eggs of *Heliothis armiger* (Hb) (Lepidoptera: Noctuidae) in cotton in the Sudan Gezira. *Bulletin of Entomological Research* 71: 183-193.

- HAGGIS M.J. (1982) Distribution of *Heliothis armigera* eggs on cotton in the Sudan Gezira: Spatial and temporal changes in their possible relation to weather. pp 87-99 In: *Proceedings of the International Workshop on Heliothis Management*, ICRISAT Center, Patancheru, India, 15-20/11/81.
- HAGGIS, M J (1984) Distribution, frequency of attack and seasonal incidence of the African armyworm, *Spodoptera exempta* (Wlk.) (Lepidoptera: Noctuidae) with particular reference to Africa and southwestern Arabia. *Tropical Development and Research Institute Report L 69*.
- HAGGIS, M.J. (1986) Distribution of the African armyworm, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae) and the frequency of larval outbreaks in Africa and Arabia. *Bulletin of Entomological Research* 76: 151-170.
- HAGGIS, M.J. (in press) Forecasting the severity of armyworm outbreak seasons in Kenya from the previous year's rainfall. *Bulletin of Entomological Research*
- HAMMOND, A.M. & FESCEMYER, H.W. (1987) Physiological correlates in migratory noctuids. The velvetbean caterpillar as a model. *Insect Science and its Applications* 8: 581-589.
- HAN, E.N. & GATEHOUSE, A.G. (1991) Genetics of precalling period in the oriental armyworm *Mythimna separata* Walker Lepidoptera Noctuidae and implications for migration. *Evolution* 45: 1502-1510.
- HATTINGH, C.C. (1941) The biology and ecology of the armyworm (*Laphygma exempta*) and its control in South Africa. *Science Bulletin of Agriculture and Forestry, Union of South Africa No.217*, 50pp.
- HILLS, R.C. (1979) The structure of the ITCZ in equatorial Africa and its relationship to East African rainfall. *Transactions of the Institute of British Geographers* 4: 329-352.

- HUTCHINS, S.H. SMELDER, R.B. & PEDIGO, L.P. (1988) Insect migration: atmospheric modeling and industrial application of an ecological phenomenon. *Bulletin of the Entomological Society of America*. 34: 9-16.
- HUTCHINSON, P. (1992) The Southern Oscillation and prediction of 'Der' season rainfall in Somalia. *Journal of Climate* 5: 525-531.
- JANSSEN, J.A.M. (1993) Soil nutrient availability in a primary outbreak area of the African armyworm, *Spodoptera exempta* (Lepidoptera: Noctuidae), in relation to drought intensity and outbreak development in Kenya. *Bulletin of Entomological Research* 83: 579-593.
- JANSSEN, J.A.M. & ROSE, D.J.W. (1990) Does the nutritional quality of the larval host plants influence the occurrence of the outbreaks of the African armyworm? *International Symposium on Crop Protection, Meded Faculte Landbouwwet Rijksuniv Gent* 55 (2 Part A); 289-296.
- JANSSEN, J.A.M. & ROSE, D.J.W. (1991) The effect of nutrition on outbreaks of the African armyworm *Spodoptera exempta* Walker. *Symposia Biologica Hungarica* 39: 481-484.
- JOHNSON, C.G. (1969) *Migration and dispersal of insects by flight*. Methuen, London.
- JOHNSON, D.H. (1962) Rain in East Africa. *Quarterly Journal of the Royal Meteorological Society* 88: 1-19.
- JOHNSON, D.H. & MOERTH, H.T. (1963) Forecasting research in East Africa. pp56-137 In: *Tropical meteorology in East Africa. Proceedings of a symposium sponsored by WMO and the MUNITALP Foundation*.
- JOHNSON, S.J. (1987) Migration and the life history strategy of the fall armyworm *Spodoptera frugiperda* in the western hemisphere. *Insect Science and its Applications* 8: 543-549.

- KENNEDY, J.S. (1961) A turning point in the study of insect migration. *Nature* 189: 785-791.
- KENNEDY, J.S. (1985) Migration, behavioral and ecological. pp5-26 In: *Migration: Mechanisms and Adaptive Significance*. Ed. M.A.Rankin. *Contributions in marine science*, University of Texas, Austin. 868pp.
- KENYA METEOROLOGICAL DEPARTMENT (1984) *Climatological statistics for Kenya*.
- KING, A.B.S., ARMES, N.J. & PEDGLEY, D.E. (1990) A mark-capture study of *Helicoverpa armigera* dispersal from pigeonpea in southern India. *Entomologia Experimentalis Applicata* 55: 257-266.
- KINUTHIA, J.H. & ASNANI, G.C. (1982) A newly found jet in North Kenya (Turkana Channel). *Monthly Weather Review* 110: 1722-1728.
- KOMAROVA, O.S. (1959) The formation of the overwintering population and the diapause of the pupae of the cotton noctuid. *Review Entomology URSS* 38: 352-360.
- KUHNEL, J. (1991) Cloudiness fluctuations over eastern Africa. *Meteorology and Atmospheric Physics* 46: 185-195.
- LANGER, H. & ROSE, D.J.W. (1986) A high density field population of mixed phases (*solitaria* and *gregaria*) of armyworm (*Spodoptera exempta*) caterpillars in Kenya. *Experimental Biology* 45: 275-278.
- LAWRENCE, E. (1989) *Henderson's Dictionary of Biological Terms*. Longman Scientific & Technical, Harlow. 637pp.
- LI K-P, WONG H-H, WOO W-S (1964) Route of the seasonal migration of the oriental armyworm moth in the eastern part of China as indicated by a three year result of releasing and recapturing of marked moths. *Acta Phytophylactica Sinica* 3: 101-110.
- LUMB, F.E. (1970) Topographic influences on thunderstorm activity near Lake Victoria. *Weather* 25: 404-410.

- MACARTHUR R H & WILSON E O (1967) *The theory of Island Biogeography*. Princeton University Press, Princeton.
- MARTIN, D.W. & HOWLAND, M.R. (1986) Grid history: A geostationary satellite technique for estimating daily rainfall in the tropics. *Journal of Climate and Applied Meteorology* 25: 184-195.
- MAURER, B.A. (1994) *Geographical population analysis: tools for the analysis of biodiversity. Methods in Ecology Series, Blackwell Scientific Publications, London. 130pp.*
- MCCAFFERY, A.R., KING, A.B.S., WALKER, A.J., EL-NAYIR, H. (1989) Resistance to synthetic pyrethroids in the bollworm, *Heliothis armigera* from Andhra Pradesh, India. *Pesticide Science* 27: 65-76.
- MCDONALD, G., BRYCESON, K.P. & FARROW, C.P. (1990) The development of the 1983 outbreak of the common armyworm *Mythimna convecta* in eastern Australia. *Journal of Applied Ecology* 27: 1001-1019.
- MCNEIL, J.N. (1987) The true armyworm *Pseudaletia unipuncta*. A victim of the pied piper or a seasonal migrant? *Insect Science and its Applications* 8: 591-597.
- MIKKOLA, K. & SALMENSUU, P. (1965) Migration of *Laphygma exigua* Hb (Lepidoptera: Noctuidae) in northwestern Europe in 1964. *Annales Zoologica Fennici* 2: 124-139.
- MILFORD, J.R. (1989) Satellite monitoring of the Sahel. *Weather* 44: 77-82.
- MILFORD, J.R. & DUGDALE, G. (1989) Estimation of rainfall using geostationary satellite data. In: *Applications of Remote Sensing in Agriculture. Proceedings of the 48th Easter School in Agricultural Science, University of Nottingham, July 1989. Butterworth London.*

- MILFORD, J.R. & DUGDALE, G. (1991) Rainfall monitoring (Somalia) project conclusion report. Overseas Development Administration/ University of Reading Report.
- MOERTH, H. (1970) A study of the areal and temporal distribution of rainfall anomalies in East Africa. *Proceedings of the Symposium in Tropical Meteorology, Honolulu.*
- MWANDOTO, S.H. (1993) Rainfall estimation using infrared Meteosat imagery by the cloud pattern recognition technique and the application to monitoring of armyworm outbreaks in east Africa. A thesis submitted in part fulfilment for a PhD, University of Nairobi, May 1993.
- NAKAMURA, K. (1967) Climate of East Africa as related to equatorial westerlies. *Geographical Reports of the Tokyo Meteorological University* 2: 49-69.
- NAKAMURA, K. (1968) Equatorial westerlies over East Africa and their climatological significance. *Geographical Reports Tokyo Meteorological University* 3: 43-60.
- NASR, E.A., TUCKER, M.R. & CAMPION, D.G. (1984) Distribution of moths of the Egyptian cotton leafworm *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae), in the Nile Delta, interpreted from catches in a pheromone trap network in relation th meteorological factors. *Bulletin of Entomological Research* 74: 487-494.
- NIEUWOLT, S. (1974) Rianstorm distribution in Tanzania. *Geografiska Annaler* 56A: 241-250.
- NICHOLSON, S.E. & ENTEKHABI, D. (1986) The quasi-period behavior of rainfall variability in Africa and its relationship to the Southern Oscillation. *Archive for Meteorology, Geophysics and Bioclimatology Series A.* 34: 311-348.

- NYAMBO, B.T. (1986) Studies in the bollworm, *Heliothis armigera* Hubner, the key cotton pest in Tanzania, as a basis for improved integrated pest management. PhD thesis, University of London. 444pp.
- NYIRENDA, G.K.C. (1985) Persistent populations of males of the African armyworm *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae) in Malawi. *Bulletin of Entomological Research* 75: 405-415.
- ODIYO, P.O. (1975) Seasonal distribution and migrations of *Agrotis ipsilon* (Huffner) (Lepidoptera: Noctuidae). *Tropical Pest Bulletin* 4: Centre for Overseas Pest Research. 26pp.
- ODIYO, P. O. (1979) Forecasting infestations of a migrant pest: the African armyworm *Spodoptera exempta* (Walker). *Philosophical Transactions of the Royal Society, London* B287: 403-413.
- ODIYO, P. O. (1981) Development of the first outbreaks of the African armyworm, *Spodoptera exempta* (Walker) between Kenya and Tanzania during the 'off-season' months of July-December. *Insect Science and its Application* 1: 305-318.
- ODIYO, P. O. (1984) A guide to seasonal changes in the distribution of armyworm infestations in East Africa. *Insect Science and its Application* 5: 107-119.
- ODIYO, P.O. (1987) The use of biogeographical techniques in the study of migrant noctuid moths. *Insect Science and its Application* 8: 551-559.
- OGALLO, L.J. (1988) Relationships between seasonal rainfall in east Africa and the Southern Oscillation. *Journal of Climatology* 8: 31-46.
- PAGE, W. W. (1988) Varying durations of arrested oocyte development in relation to migration in the African armyworm moth, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae). *Bulletin of Entomological Research* 79: 181-198.

- PALMER, C., WISE, C., STEMPSON, L. & DUNCAN, C. (1955)
The practical aspects of tropical meteorology. *Air Forces Surveys in Geophysics No 76* 195pp + Figs.
- PAIR, S.D., RAULSTON, J.R., RUMMEL, D.R., WESTBROOK, J.K., WOLF, W.W., SPARKS, A.N. & SCHUSTER, M.F. (1987) Development and production of corn earworm and fall armyworm in the Texas USA high plains, evidence for a reverse fall migration. *Southwestern Entomologist* 12: 89-99.
- PANT, P.S. & RWANDUSYA, E.M. (1971) Climates of East Africa. *East African Meteorological Department Technical Memoir No.18*. Nairobi. 11pp.
- PARKER, W .E. & GATEHOUSE, A. G. (1985a) The effect of larval rearing conditions on flight performances in females of the African armyworm, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae). *Bulletin of Entomological Research* 75: 35-47.
- PARKER, W.E. & GATEHOUSE, A.G. (1985b) Genetic factors controlling flight performance and migration in the African armyworm moth, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae). *Bulletin of Entomological Research* 75: 49-63.
- PEDGLEY, D.E. (1982) *Windborne pests and diseases. Meteorology of airborne organisms*. Ellis Horwood Ltd. Chichester/John Willey & Sons.
- PEDGLEY, D.E. (1985) Windborne migration of *Heliothis armigera* (Hubner)(Lepidoptera: Noctuidae) to the British Isles. *Entomologist's Gazette* 36: 15-20.
- PEDGLEY, D.E. (1986) Windborne migration in the Middle East by the moth *Heliothis armigera* (Lepidoptera: Noctuidae). *Ecological Entomology* 11: 467-470.
- PEDGLEY, D.E. (1990) Concentration of flying insects by the wind. In: *Migrant pests: problems, potentialities and progress*. *Philosophical Transactions of the Royal Society, London*. B328: 631-653.

- PEDGLEY, D.E. REYNOLDS, D.R., RILEY, J.R. & TUCKER, M.R. (1982) Flying insects reveal small-scale wind systems. *Weather* 37: 295-306.
- PEDGLEY, D.E., PAGE, W.W., MUSHI, A., ODIYO, P., AMISI, J., DEWHURST, C.F., DUNSTAN, W.R., FISHPOOL, L.D.C., HARVEY, A.W., MEGENASA, T. & ROSE D.J.W. (1989) Onset and spread of an African armyworm upsurge. *Ecological Entomology* 14: 311-333.
- PEDGLEY, D.E., TUCKER, M.R. & PAWAR, C.S. (1987) Windborne migration of *Heliothis armigera* (Hubner)(Lepidoptera: Noctuidae) in India. *Insect Science and its Applications*. 8: 599-604.
- PERSSON, B. (1981) Population fluctuations of the African armyworm (*Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae) in outdoor cages in Kenya. *Bulletin of Entomological Research* 71: 289-297.
- PORCU, F. & LEVIZZANI, V. (1992) Cloud classification using Meteosat VIS-IR imagery. *International Journal of Remote Sensing* 13: 893-909.
- RAINEY, R.C. (1951) Weather and the movements of locust swarms: a new hypothesis. *Nature*, London 168: 1057-1060.
- RAINEY, R.C. (1963) Meteorology and the migration of desert locusts. *World Meteorological Organisation Technical Note No. 54 / Antilocust Memoir No. 7*.
- RAINEY, R.C. (1989) *Migration and meteorology- Flight behaviour and the atmospheric environment of locusts and other migrant pests*. 314pp. Oxford Science publications, Clarendon Press, Oxford.
- RAINEY, R.C. & BETTS, E. (1979) Problems of alternative hypotheses: Continuity in major populations of migrant pests: the desert locust and the African armyworm. *Philosophical Transactions of the Royal Society, London B.287*: 359-374.

- RAULSTON, J.R., WOLF, W.W., LINGREN, P.D. & SPARKS, A.N. (1982) Migration as a factor in *Heliothis* management. pp 61-73. In: *Proceedings of the International Workshop on Heliothis Management*, 15-20 Nov. 1981, Patencheru. ICRISAT.
- RAULSTON, J.R., PAIR, S.D., MARTINEZ, F., WESTBROOK, J., SPARKS, A. & VALDEZ, V. (1986) Ecological studies indicating the migration of *Heliothis zea*, *Spodoptera frugiperda* and *Heliothis virescens* from northeastern Mexico and Texas USA. In: Danthanarayana, W. (Ed). *Insect Flight: Dispersal and Migration*. 289pp.
- REED, W. (1965) *Heliothis armigera* (Hubner) (Noctuidae) in western Tanganyika. 1. Biology with special reference to the pupal stage. *Bulletin of Entomological Research* 56: 117-125.
- REYNOLDS, D.R. & RILEY, J.R. (1988) A migration of grasshoppers, particularly *Diaboloocatantops axillaris* (Thunberg) (Orthoptera: Acrididae), in the West African Sahel. *Bulletin of Entomological Research* 78: 251-271.
- RIEHL, H. (1979) *Climate and weather in the tropics*. 611pp. Academic Press.
- RILEY, J.R., ARMES, N.J., REYNOLDS, D.R. & SMITH, A.D. (1992) Nocturnal observations on the emergence and flight behaviour of *Helicoverpa armigera* (Lepidoptera: Noctuidae) in the post-rainy season in central India. *Bulletin of Entomological Research* 82: 243-256.
- RILEY, J.R. & REYNOLDS, D.R. (1983) A long-range migration of grasshoppers observed in the Sahelian zone of Mali by two radars. *Journal of Animal Ecology* 52: 167-183.

- RILEY, J.R., REYNOLDS, D.R. & FARMERY, M.J. (1983) Observations of the flight behaviour of the armyworm moth, *Spodoptera exempta* at an emergence site using radar and infra-red optical techniques. *Ecological Entomology* 8: 395-418.
- RILEY, J.R., REYNOLDS, D.R. & FARROW, R.A. (1987) The migration of *Nilaparvata lugens* (Stal)(Delphacidae) and other Hemiptera associated with rice during the dry season in the Philippines: a study using radar, visual observations, aerial netting and ground trapping. *Bulletin of Entomological Research* 77: 145-169.
- RILEY, J.R., CHENG, X.N., ZHANG, X.X., REYNOLDS, D.R., XU, G.M., SMITH, A.D., CHENG, J.Y., BAO, A.D. & ZHAI, B.P. (1991) The long-distance migration of *Nilaparvata lugens* (Stal)(Delphacidae) in China: radar observations of mass return flight in the autumn. *Ecological Entomology* 16: 471-489.
- RIVNAY, E. (1961) The phenology of *Prodenia litura* F. in Israel with reference to its occurrence in the Near East at large. *Bulletin of the Research Council of Israel* 10B: 100-106.
- ROBINSON, T.P. (1991) Modelling the seasonal distribution of habitat suitability for armyworm population development in east Africa using GIS and remote sensing techniques. *PhD thesis, University of Reading*. 362pp.
- RODHE, H. & VIRJI, H. (1976) Trends and periodicities in East African rainfall data. *Monthly Weather Review* 104: 307-315.
- ROGERS, D.J. (1991) Satellite imagery, tsetse and trypanosomiasis in Africa. *Preventative Veterinary Medicine* 11: 201-220.
- ROGERS, D.J. & RANDOLPH, S.E. (1991) Mortality rates and population density of tsetse flies correlated with satellite imagery. *Nature* 351: 739-741.

- ROOME, R.E. (1979) Pupal diapause in *Heliothis armigera* (Hubner)(*Lepidoptera:Noctuidae*) in Botswana: its regulation by environmental factors. *Bulletin of Entomological Research* 69: 149-160.
- ROPELEWSKI, C.F. & HALPERT, M.S. (1987) Global and regional- scale precipitation patterns associated with the El Nino/ Southern Oscillation. *Monthly Weather Review* 115: 1606-1626.
- ROSE, D.J.W. (1975) Field development and quality changes in successive generations of *Spodoptera exempta* Wlk; the African armyworm. *Journal of Applied Ecology* 12: 727-739.
- ROSE, D.J.W. (1979) The significance of low-density populations of the African armyworm *Spodoptera exempta* (Wlk). *Philosophical Transactions of the Royal Society, London B287*: 393-402.
- ROSE, D.J.W. & DEWHURST, C.F. (1979) The African armyworm, *Spodoptera exempta* - congregation of moths in trees before flight. *Entomologia experimentalis et applicata* 26: 346-348.
- ROSE, D.J.W. & LAW, A.B. (1976) The synoptic weather in relation to an outbreak of the African armyworm (*Spodoptera exempta* Walker)(in Rhodesia) *Journal of the Entomological Society of South Africa* 39: 125-130.
- ROSE, D.J.W., ILES, M.J. & WARD, A. (1988) Cereal losses caused by armyworm in eastern and southern Africa: current information and research proposals. *Insect Science and its Application* 9: 697-699.
- ROSE, D.J.W., PAGE, W.W., DEWHURST, C.F., RILEY, J.R., REYNOLDS, D.R., PEDGLEY, D.E. & TUCKER, M.R. (1985) Downwind migration of the African armyworm moth, *Spodoptera exempta*, studied by mark-and-capture and by radar. *Ecological Entomology* 10: 299-313.

- ROSE, D.J.W., DEWHURST, C.F., PAGE, W.W. & FISHPOOL, L. D.C. (1987) The role of migration in the life system of the African armyworm *Spodoptera exempta*. *Insect Science and its Application* 8: 561-569.
- ROSENBERG, L.J. & MAGOR, J.I. (1987) Predicting windborne displacements of the brown planthopper, *Nilaparvata lugens* from synoptic weather data. 1. Long-distance displacements in the north-east monsoon. *Journal of Animal Ecology* 56: 39-51.
- SAPPINGTON, T.W. & SHOWERS, W.B. (1992) Reproductive maturity, mating status and long-duration flight behavior of *Agrotis ipsilon* (Lepidoptera: Noctuidae) and the conceptual misuse of the oogenesis-flight syndrome by entomologists. *Environmental Entomology* 21: 677-688.
- SCOTT, P. J. (1991) A general review of the evidence on the economic importance of the African armyworm (with specific reference to the eastern Africa region). *DLCO-EA Technical Report No. 100*.
- SHARON, D. (1974) The spatial pattern of convective rainfall in Sukumaland Tanzania- a statistical analysis. *Archive for Meteorology Geophysics and Bioclimatology Series B* 22: 201-218.
- SHOWERS W B, KEASTER A J, RAULSTON J R, HENDRIX iii, W H, DERRICK M E, MCCORCLE M D, ROBINSON J F, WAY M O, WALLENDORF M J & GOODENOUGH J L. (1993) Mechanism of southward migration of a noctuid moth [*Agrotis ipsilon* (Hufnagel)] a complete migrant. *Ecology* 74: 2303-2314.
- SHOWERS, W.B., SMELSER, R.B., KEASTER, A.J., WHITFORD, F., ROBINSON, J.F., LOPEZ, J.D. & TAYLOR, S.E. (1989) Recapture of marked black cutworm (*Lepidoptera: Noctuidae*) males after long-range transport. *Environmental Entomology* 18: 447-458.

- SMELSER, R.B., SHOWERS, W.B., SHAW, R.H. & TAYLOR, S.E. (1991) Atmospheric trajectory analysis to project long-range migration of black cutworm *Lepidoptera Noctuidae* adults. *Journal of Economic Entomology* 84: 879-885.
- SOUTHWOOD, T.R.E. (1977) Habitat, the tenplet for ecological strategies ? *Journal of Animal Ecology* 46: 337-365.
- SUMNER, G.N. (1981) The nature and development of rainstorms in coastal East Africa. *Journal of Climatology* 1: 131-152.
- SUMNER, G.N. (1983) Daily rainfall variability in coastal Tanzania. *Geografiska Annaler Series A* 65: 53-66.
- SUMNER, G.N. (1984) The impact of wind circulation on the incidence and nature of rainstorms over Dar es Salaam, Tanzania. *Journal of Climatology* 4: 35-52.
- TAYLOR, L.R. (1958) Aphid dispersal and diurnal periodicity. *Proceedings of the Linnean Society, London*. 169: 69-73.
- TAYLOR, L.R. (1960) The distribution of insects at low levels in the air. *Journal of Animal Ecology* 29: 45-63.
- TAYLOR, L.R. (1974) Insect migration, flight periodicity and the boundary layer. *Journal of Animal Ecology* 43: 225-238.
- TAYLOR, L.R., FRENCH, R.A. & MACAULAY, E.D.M. (1973) Low altitude migration and diurnal flight periodicity; the importance of *Plusia gamma* Linneaus (Lepidoptera: Plusiidae) *Journal of Animal Ecology* 42: 751-760.
- TAYLOR, R.A.J. (1986) Time series analysis of numbers of Lepidoptera caught at light traps in East Africa and the effect of moonlight on trap efficiency. *Bulletin of Entomological Research* 76: 593-606.
- TOMSETT, J.E. (1969) Average monthly and annual rainfall maps of East Africa. *East African Meteorological Department Technical Memoir No. 14*.

- TOMSETT, J.E. (1975) The diurnal variation of precipitation in East Africa. *East African Meteorological Department Technical Memorandum No.25.*
- TOPPER, C.P. (1987) The dynamics of the adult population of *Heliothis armigera* (Hubner) (Lepidoptera: Noctuidae) within the Sudan Gezira in relation to cropping pattern and pest control in cotton. *Bulletin of Entomological Research* 77: 525-539.
- TOPPER, C.P. (1987) Nocturnal behaviour of adults *Heliothis armigera* (Hubner)(Lepidoptera:Noctuidae) in the Sudan Gezira and pest control implications. *Bulletin of Entomological Research* 77: 541-554.
- TRAPNELL, C.G. & LANGDALE-BROWN, I. (1962) The natural vegetation of East Africa. In: *The Natural Resources of East Africa* (Edited by Russell, E.W.) pp 92-102.
- TREWARTHA, G.T. (1981) *The Earth's Problem Climates* (revised edition). University of Wisconsin Press. Methuen & Co.Ltd, London 371pp.
- TUCKER, M.R., MWANDOTO, S. & PEDGLEY, D.E. (1982) Further evidence for windborne movement of armyworm moths, *Spodoptera exempta*, in East Africa. *Ecological Entomology* 7: 463-473.
- TUCKER, M.R. & PEDGLEY, D.E. (1983) Rainfall and outbreaks of the African armyworm *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae). *Bulletin of Entomological Research* 73: 195-199.
- TUCKER, M.R. (1984a) Possible sources of outbreaks of the armyworm, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae) in East Africa at the beginning of the season. *Bulletin of Entomological Research* 75: 599-607.
- TUCKER, M. R. (1984b) Forecasting the severity of armyworm seasons in East Africa from early season rainfall. *Insect Science and its Application* 5: 51-55.

- TUCKER, M.R. (1993) Weather and the epidemiology of the African armyworm (*Spodoptera exempta*). *NRI Bulletin* No.58. 70pp
- TUCKER, M.R. (1994) Inter- and intra-seasonal variation in outbreak distribution of the armyworm, *Spodoptera exempta* (Walker)(Lepidoptera: Noctuidae), in eastern Africa. *Bulletin of Entomological Research* 84: 275-287.
- TUNSTALL, J.P. (1968) Pupal development and moth emergence of the red bollworm (*Diparopsis castanae* Hmps) in Malawi. *Bulletin of Entomological Research* 58: 233-254.
- TUNSTALL, J.P. (1958) The biology of the Sudan bollworm, *Diparopsis watersii* (Roths) in the Gash delta, Sudan. *Bulletin of Entomological Research* 49: 1-23.
- VAN DE BOOGAARD, H.M.E. & RAO, G.V. (1984) Mesoscale structure of the low-level flow near the Equatorial East African coast. *Monthly Weather Review* 112: 91-107.
- WALOFF, Z. (1972) Orientation of flying locusts, *Schistocerca gregaria* (Forsk.) in migrating swarms. *Bulletin of Entomological Research* 62: 1-72.
- WILLIAMS, C.B. (1958) *Insect Migration*, Collins, London. 235pp.
- WILSON, K. & GATEHOUSE, A.G. (1992) Migration and genetics of pre-reproductive period in the moth *Spodoptera exempta*, African armyworm. *Heredity* 69: 255-262.
- WILSON, K. & GATEHOUSE, A.G. (1993) Seasonal and geographical variation in the migratory potential of outbreak populations of the African armyworm moth, *Spodoptera exempta*. *Journal of Animal Ecology* 62: 169-181.

- WOLF, R.A., PEDIGO, L.P., SHAW, R.H. & NEWSOM, L.D. (1987) Migration - transport of the green cloverworm *Plathypena scabra* F. Lepidoptera Noctuidae into Iowa USA as determined by synoptic-scale weather patterns. *Environmental Entomology* 16: 1169-1174.
- WOLF, W.W., WESTBROOK, J.K., RAULSTON, J., PAIR, S.D. & HOBBS, S.E. (1990) Recent airborne radar observations of migrant pests in the USA. *Philosophical Transactions of the Royal Society, London. B. Biological Science* 328: 619-630.
- WOODROW, K.P., GATEHOUSE, A.G. & DAVIES, D.A. (1987) The effect of larval phase on flight performance of African armyworm moths *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae). *Bulletin of Entomological Research* 77: 113-122.
- YARRO, J.G. (1984) Life and fertility tables for *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae). *Insect Science and its Application* 5: 303-305.
- YARRO, J.G., OTINDO, B.L., GATEHOUSE, A.G. & LUBEGA, M.C. (1981) Dwarf variety of coconut, *Cocos nucifera* (Palmae), a hostplant for the African armyworm, *Spodoptera exempta* (Walker) (Lepidoptera, Noctuidae). *Insect Science and its Application* 1: 362-363.

APPENDIX

Armyworm seasons are summarized in maps showing primary (bold numerals) and secondary outbreaks, by the month in which an outbreak first occurred in a degree square. Later outbreaks in that degree square are not shown, for reasons of clarity. Moth migrations between outbreaks are shown by solid arrows where they are indicated by trajectory analysis, and by broken arrows where data were inadequate for such analyses and the results were more uncertain.

The text summarizes the occurrence of primary and secondary outbreaks for each season and the associated rainfall, windfields and deduced moth migrations. Tables 8 and 9 give examples of the distribution of rainstorms in relation to particular outbreaks, and examples are given of particular moth trajectories and windfields. The aim is to facilitate the direct comparison of armyworm seasons and to highlight some of the main features of each season. This appendix may also give some guidance to the armyworm forecaster in the analysis of current armyworm seasons.

Seasonal summaries

(i) 1972-73 (Fig 37)

Brief Summary

A very low armyworm season, with only one early outbreak and heavy early rains. There were unusual late-season armyworm outbreaks in east-central and north-east Tanzania but no known secondary outbreaks.

Primary outbreaks

There were no early outbreaks in the main primary outbreak areas, but there was a single primary outbreak (of 60ha) near Kisumu (western Kenya) in December. In areas where early season outbreaks usually occur (Kenya south of the equator and eastern and central Tanzania) rainfall was well above average in October and November (Table 13). In December it was also above average in most of Tanzania but not in the north or in Kenya. Nearly all the Kenyan stations had 10 or more raindays in November and these frequent rains may have caused poor larval survival.

Armyworm at low density were present from December 1972-February 1973 judging by moth catches at Muguga and the National Agricultural Laboratories, Nairobi, Kenya and at Tengeru, Arusha TPRI and Ilonga, Tanzania. Following very low catches in March and April, catches increased at Tengeru, Ilonga and Morogoro on 8 May and these were associated with outbreaks near Moshi (north-east Tanzania), Ilonga, Morogoro (east-central Tanzania) and Kisarawe (near Dar es Salaam) in May. These unusually late Tanzanian outbreaks may have been caused either by local build-up or by moth migration on southerly winds. Although no outbreak sources were known in southern

Figure 37. Seasonal summary map for 1972-73 showing the location of primary armyworm outbreaks by month of first occurrence in a degree square. There were no secondary outbreaks.

1972-73

30E

35E

40E

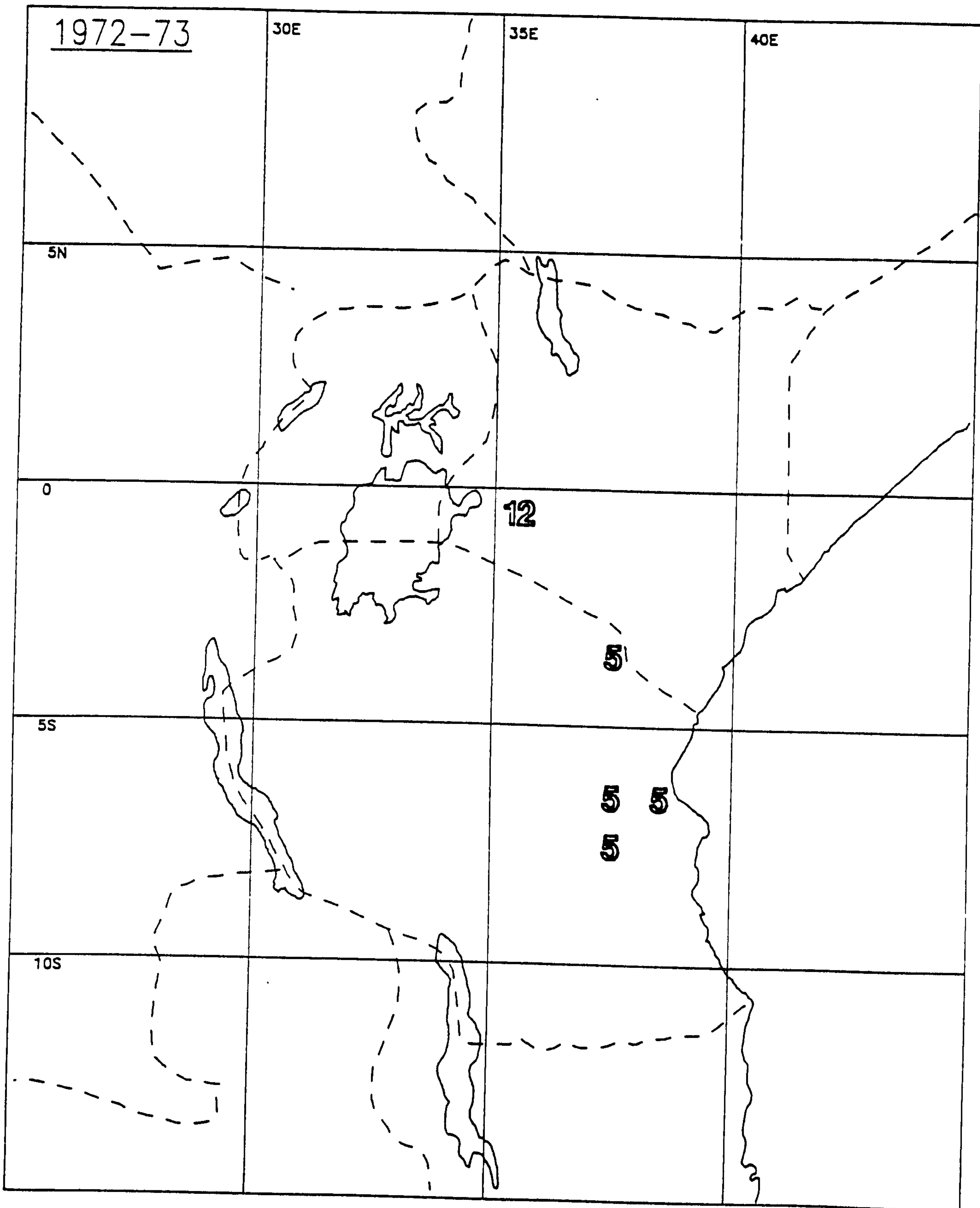
5N

0

12

5S

10S



	OCTOBER			NOVEMBER			DECEMBER		
	MONTH MEAN mm	1972 %OF MEAN RAINDAYS	1972 MEAN mm	MONTH MEAN mm	1972 %OF MEAN RAINDAYS	1972 MEAN mm	MONTH MEAN mm	1972 %OF MEAN RAINDAYS	1972 MEAN mm
KENYA									
Mombasa	96	341	11	95	88	9	70	80	6
Voi	26	42	5	106	202	11	119	97	9
Makindu	28	11	3	172	137	10	115	65	6
Machakos	52	331	11	193	81	12	122	49	8
Nairobi	38	426	9	134	72	10	74	34	7
Kisumu	75	203	14	120	188	17	100	62	6
TANZANIA									
Arusha	25	44	3	139	143	13	93	52	7
Same	30	140	5	53	228	12	67	72	7
DaresSalaam	60	220	11	122	144	11	108	125	7
Morogoro	29	286	7	61	116	8	78	137	6
Kilosa	33	303	4	96	238	8	139	99	5
Dodoma	4	350	1	20	195	4	107	191	5
Mlwara	21	119	6	53	70	5	192	166	16
Nachingwea	7	14	0	70	127	6	126	133	11

Table 13. Monthly rainfall as a percentage of the mean and number of raindays in Kenya and Tanzania, October-December 1972.

Tanzania, an increase in trap catches at Mbeya (south-west Tanzania) from 27 April shows that armyworm were present there.

(ii) 1973-74 (Fig.38)

Brief Summary

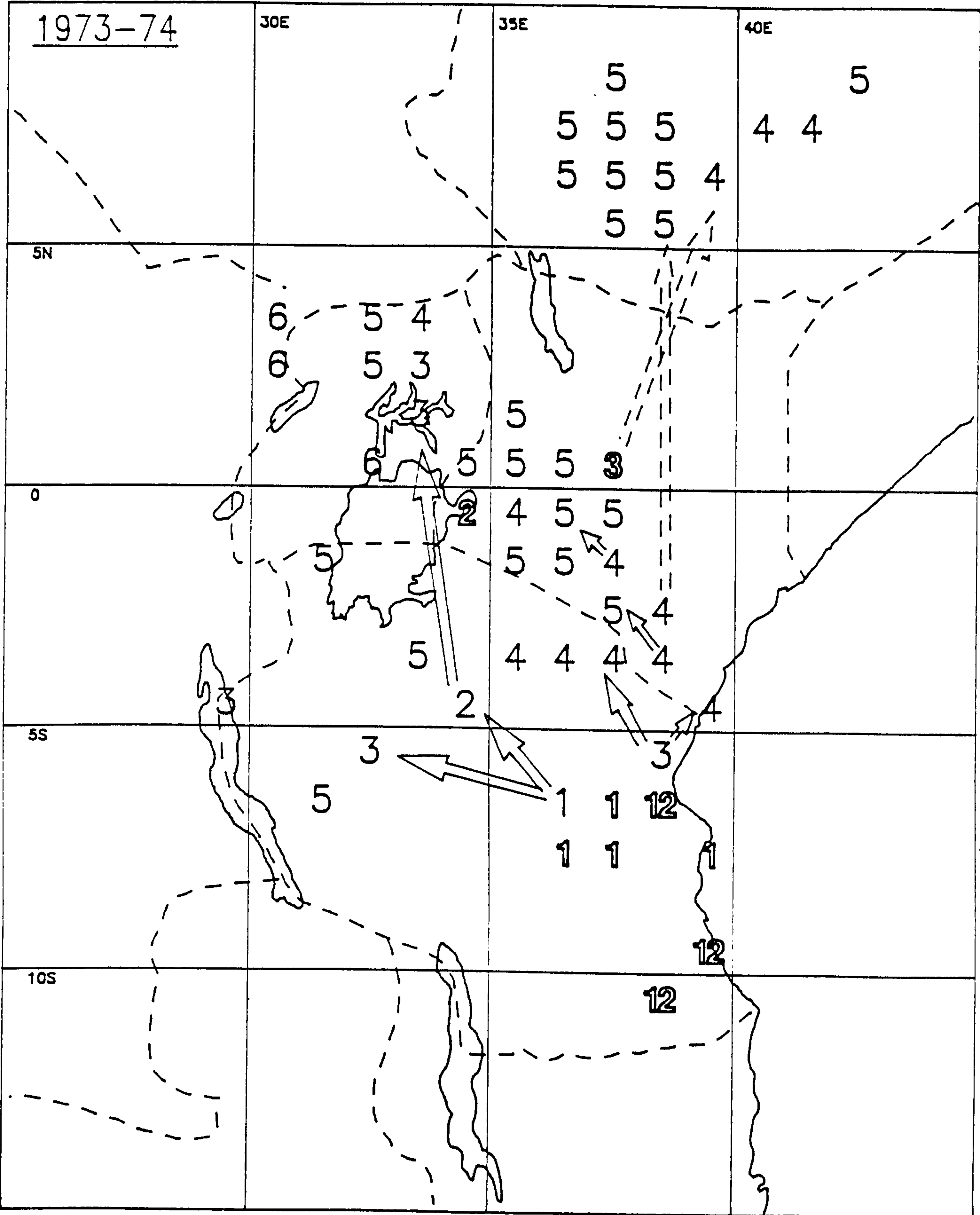
A moderate season, starting late in Tanzania with migrations from central Tanzania to Uganda in March, and northern Tanzania to east-central Kenya and southern Ethiopia in May. In Kenya and Ethiopia outbreaks were most severe in May-June but there were also widespread outbreaks in south-east Tanzania at the beginning of the season. Rains, starting late, in December, in Tanzania, and a dry spell in May during the long rains in Kenya, helped armyworm survival and contributed to large outbreaks.

Primary outbreaks

The first outbreaks occurred in Kilwa, Lindi and Nachingwea districts (south-east Tanzania) and near Dar es Salaam (central Tanzanian coast) in mid-late December. The south-east Tanzanian outbreaks were large, although the reported total area of >600000 ha was probably an exaggeration. Outbreak sources were probably local, low density populations because winds were onshore easterlies with a brief incursion of westerly winds being confined to south-west Tanzania.

Four outbreaks in Morogoro region (east-central Tanzania) (about 400ha) and one on Mafia Island (central Tanzanian coast) (1000ha) in early January were probably also primary since the former were too early to be derived from the December coast primary, and the latter was

Figure 38. Seasonal summary map for 1973-74 showing primary (bold numerals) and secondary armyworm outbreaks by month of first occurrence in a degree square, and likely migrations between outbreaks from trajectory analyses.



south-east of that outbreak, while winds were towards the west.

Rainfall was below average in eastern Tanzania in October and November. December outbreaks of armyworm were associated with isolated rainstorms in the middle of the month, and moths leading to early-January outbreaks were probably concentrated by widespread rainstorms in the Morogoro region on 14 January (Table 14).

Late primary outbreaks (about 300ha) occurred in south Nyanza (western Kenya) in mid-February, associated with isolated rainstorms, and at Meru (east-central Kenya) (about 25ha) in March, associated with the beginning of the Long rains on 19 March. Backtracks from south Nyanza came from northern Tanzania, and those from Meru from eastern Kenya. There were no known earlier outbreaks in either source area.

Secondary outbreaks

An outbreak at Mpwapwa (east-central Tanzania) in late January probably originated from moths flying westwards from the Dar es Salaam primary. Outbreaks in Singida and Morogoro regions in February almost certainly came from moths migrating north-westwards from Morogoro outbreaks (Fig.38). Further westward migrations from east-central Tanzania gave rise to a small outbreak at Tabora, and southerly winds on 21-22 March near the coast may have taken moths to the Tanga region where there were two outbreaks with moth arrival in late March.

From the Singida outbreaks, trajectories indicated migration northwards across Lake Victoria to Uganda, with high moth catches near Mwanza and strong south-easterly winds across the lake. Widespread outbreaks (>3000ha) in Uganda in mid-March probably originated from this

OUTBREAK LOCATION	RAINFALL STATION	DATE						
		1	5	10	15	20	25	30
MVOMERO 0620S 3725E	Mvomero		X	X				
	Berega mission				X	X	X	X
	Chazi				X			
	Wami prison			X			X	X
	Magubika						X	X
MIKUMI 0724S 3659E	Mikumi			X		X		
	Ulaya			X		X	X	X
	Kisanga				X		X	X
	Kilombero			X			X	X
	Kikoboga				X	X	X	X
KISAKI 0728S 3736E BWAHIRA CHINI 0724S 3744E	Kisaki							X
	Bwikira juu							
	Bwikira est.							X
	Outhumi					X	X	X
	Singiza					X	X	X
Steiglers gorge							X	

Armyworm outbreaks
Probable moth arrival date

KEY

X ————— Estimated moth arrival
Rainfall > 9.9mm (Rainstorm)

Table 14. Rainstorms associated with primary outbreaks in the Morogoro region in January 1974.

migration. On a few days south-easterly winds may have brought moths from the February primary outbreaks in western Kenya. Further outbreaks in northern Uganda from April-June were derived from these March outbreaks.

In April there were many outbreaks (total area >8000 ha) in the Arusha and Kilimanjaro regions (north-east Tanzania) and Taita-Taveta and Kwale districts (south-east Kenya). Winds indicated that parent moths may have come from Tanga outbreaks.

These outbreaks were sources for moths invading east-central Kenya in mid-May on southerly winds. Their arrival was marked by high moth catches in the Nairobi area from 9-30 May. At this time there were approximately 75 outbreaks in east-central Kenya covering an area of about 50000 ha, and other outbreaks in north-west Kenya including one of 145000 ha.

Large, severe outbreaks occurred in southern Ethiopia in late April and May. Strong southerly winds could have brought moths from outbreaks at Meru from 20-30 April and from Taveta or Kilimanjaro in early and mid-May.

There was good armyworm survival in central Kenya in May, associated with below average rainfall, which lead to further outbreaks in central and western Kenya in June. High moth catches persisted into July even though there were no further outbreaks.

iii) 1974-75 (Fig 39)

Brief Summary

A moderate season starting in late December in south-east and east-central Tanzania. Moths migrated northward from north-east Tanzania to east-central Kenya and possibly southern Ethiopia. Outbreaks remained in Kenya until June or July associated with persistent long rains. There were no reported outbreaks in central and western Tanzania, western Kenya or Uganda, possibly due to dry weather in late January and February in central Tanzania, and successful control measures of the primary outbreaks in Morogoro region.

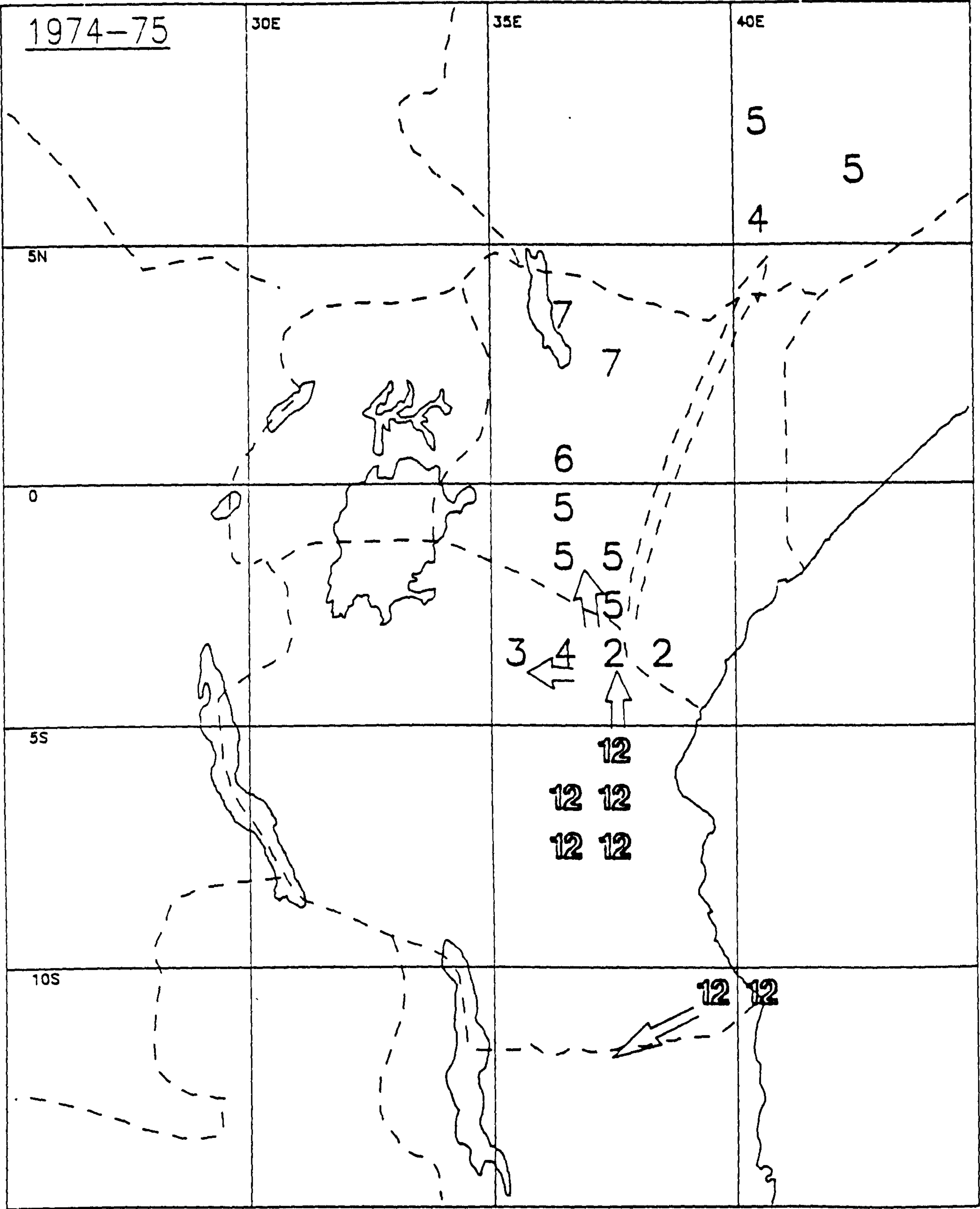
Primary outbreaks

Primary outbreaks occurred in Mtwara and Lindi regions (south-east Tanzania), in Morogoro region (east-central Tanzania) and south of Handeni (north-east Tanzania) in late December, associated with a late start to the rains. Outbreaks totalled 2500ha in south-east Tanzania and approximately the same in east-central Tanzania. They were severe in places and control was carried out.

Secondary outbreaks

There were no secondaries as a result of outbreaks in south-east or east-central Tanzania, probably because of very dry weather when the moths emerged in late January, but possibly because the control measures were successful. Outbreaks were recorded in Kilimanjaro district (north-east Tanzania) and Taita-Taveta (south-east Kenya) in February, probably derived from moths migrating on south-east winds from the Handeni outbreak. Further outbreaks near Karatu (Arusha region) occurred in March, and in Kilimanjaro region in April which were

Figure 39. Seasonal summary map for 1974-75 showing primary (bold numerals) and secondary armyworm outbreaks by month of first occurrence in a degree square, and likely migrations between outbreaks from trajectory analyses.



probably derived from the February, Kilimanjaro outbreaks. As in 1974 these late outbreaks in north-east Tanzania were followed by northward moth migration leading to outbreaks in Kajiado, Machakos, Nairobi and Nakuru districts of central Kenya in May, and possibly at Neghele in southern Ethiopia at the end of April. The migration of moths into central Kenya was recorded by large increases in catches at the Muguga light trap, associated with rainstorms from 11-16 May, and winds shifting from a north-easterly to south-easterly direction on 12 May. Moths were caught earlier at Muguga, in mid-April, possibly coming up the Rift valley from Karatu, on local southerly winds, but there were no outbreaks.

The May outbreaks in Kenya were on wild and ornamental grasses rather than crops, but some were large (6400 ha in Nakuru district and 2200 ha in Machakos district). Moths emerging from these outbreaks flew northwards to give rise to even larger outbreaks in the Samburu district in June. Above average rains in June and July were associated with persistent high moth catches at Muguga light trap until mid-July, and exceptionally late outbreaks in northern Kenya in July. The presence of south-westerly winds suggest that further outbreaks in eastern Ethiopia in June may have been derived from outbreaks at Neghele.

(iv) 1975-76 (Fig 40)

Brief Summary

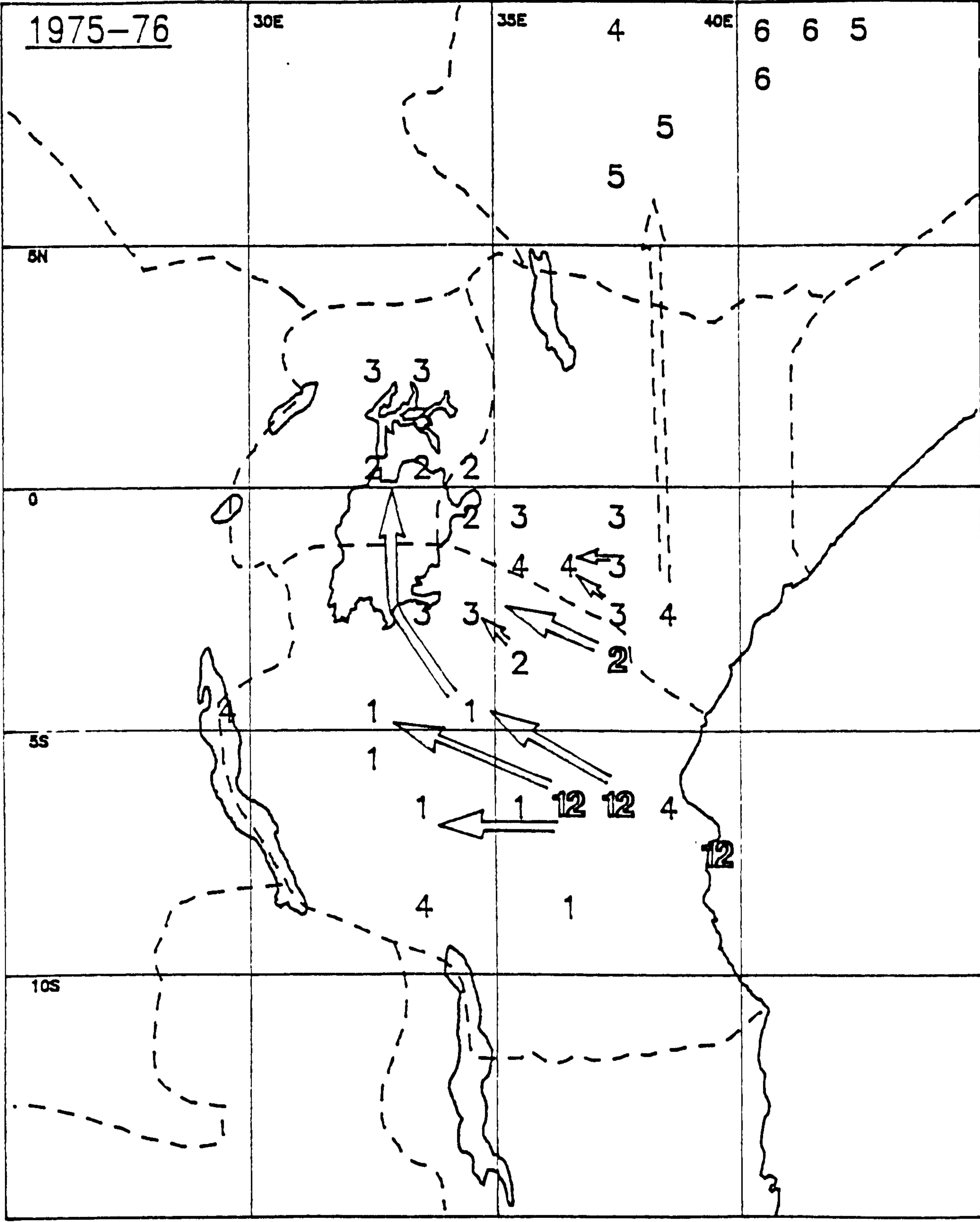
The season was of moderate severity and was associated with below average October to December rains in both Kenya and Tanzania. In Tanzania the rains started late in mid December. Primary outbreaks were also late, and few in number, but gave rise to widespread secondaries in central Tanzania and Uganda. The largest number of reported outbreaks was in western Kenya where they may have originated from unreported outbreaks in north-east Tanzania. Large outbreaks in east-central Kenya in March and April may have originated from Taveta and were associated with isolated rainstorms. Two outbreaks in May in southern Ethiopia could have originated from these outbreaks but the sources of two outbreaks in central Ethiopia in April are unknown.

Primary outbreaks

Primary outbreaks occurred over approximately 320 ha in Kilosa district (east-central Tanzania) in mid December associated with the beginning of the rains and following two dry weeks; and on the Tanzania coast, south of Dar es Salaam, in late December, about a month after the first rainstorms.

In north-east Tanzania, moth catches at Tengeru light trap, near Arusha, increased in late December and early January associated with isolated rainstorms. No outbreaks were reported until February, when there was a small outbreak in Kilimanjaro region and a larger one (260 ha) in the adjacent Taveta district of south-east Kenya. These appeared to be primary, but may have been derived from unreported outbreaks in the same areas

Figure 40. Seasonal summary map for 1975-76 showing primary (bold numerals) and secondary armyworm outbreaks by month of first occurrence in a degree square, and likely migrations between outbreaks from trajectory analyses.



associated with moth catches and isolated rainstorms in January.

Secondary outbreaks

In mid January, outbreaks occurred in the Dodoma, Tabora and Singida regions of central Tanzania, downwind of the December primaries. The outbreaks were largest in Singida region (about 2000 ha), and forward tracks (Fig. 41) together with a high trap catch at Ukiriguru (south of Lake Victoria) on 25 February, suggest that the Singida outbreaks were the sources of the outbreaks near Kawanda (central Uganda) in late February.

Scattered outbreaks over a very large area (50000 ha) at Karatu, west of Arusha, in early February may have originated in east-central Tanzania, but it is more likely that unreported outbreaks in north-east Tanzania were the source. Backtracks indicated that outbreaks in western Kenya in February (over about 3000 ha), may also have come from north-east Tanzania. These Kenya outbreaks gave rise to many large outbreaks in the same areas of western Kenya in March (over about 30000 ha).

Further east, outbreaks in Machakos district of east-central Kenya in late March were associated with large increases in moth catch in the Nairobi area (at Jacaranda, NAL and Muguga light traps) and isolated rainstorms. These were probably derived from moths migrating on south-easterly winds from Taveta.

Large outbreaks (total area about 40000 ha) occurred in Machakos and Kitui districts in late April. These were almost certainly derived from the late-March outbreaks and were associated with isolated rainstorms (Table 9). Widespread rainstorms in early April were not associated with outbreaks because moths had not emerged from late-

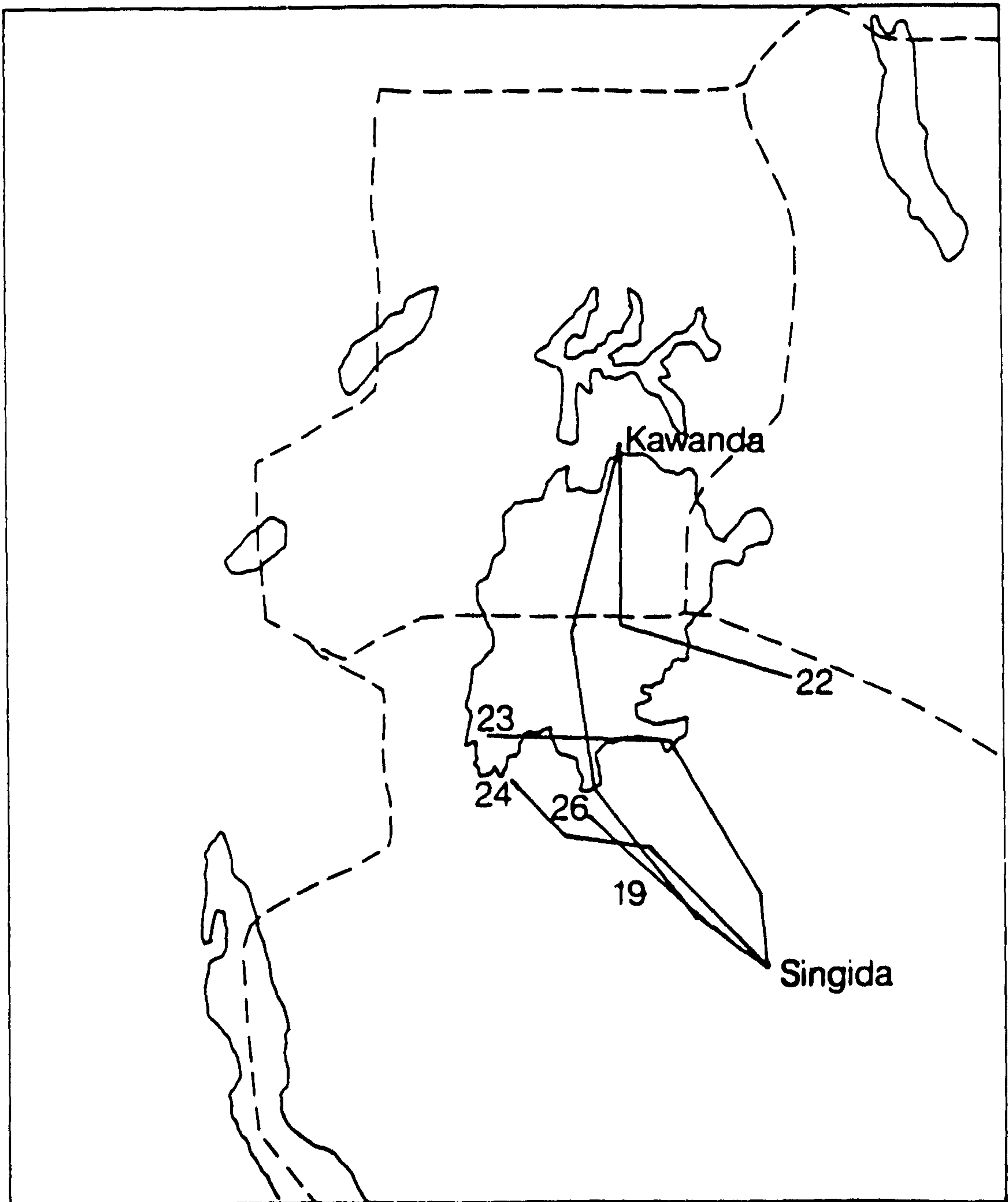


Figure 41. Backtracks from outbreaks at Kawanda and forward tracks from outbreaks at Singida for 18-24 February 1976.

March outbreaks. Moths emerging in May could have migrated northwards on strong southerly winds, and may have been the source for May outbreaks in southern Ethiopia (Fig.40). A very late outbreak at Athi River (near Nairobi) in June, almost certainly came from local outbreaks, which were the only known sources.

(v) 1976-77 (Fig.42)

Brief Summary

This severe season was associated with a late start to the rains in Tanzania. Armyworm outbreaks spread across Tanzania to Uganda from December to February following a single primary in November. It is probable that the large outbreaks in south-east Tanzania in January resulted from an unusual, large-scale moth migration from Malawi. An initial primary outbreak in east-central Kenya in November, was followed by a sequence of outbreaks in Kenya, through the dry season to March, resulting in widespread outbreaks during the long rains, and subsequent migration to Ethiopia.

Primary outbreaks

In November a primary outbreak occurred in Kilosa district (east-central Tanzania) possibly associated with an isolated rainstorm on 25 November in a dry month. In Kajiado district (east-central Kenya) a primary outbreak on pasture was associated with the beginning of the short rains on 20 November. Backtracks from both these outbreaks came from the east towards the coasts of Tanzania and Kenya respectively (Fig.9) which is typical of early season primaries in these areas.

Figure 41. Seasonal summary map for 1976-77 showing primary (bold numerals) and secondary armyworm outbreaks by month of first occurrence in a degree square, and likely migrations between outbreaks from trajectory analyses.

1976-77

30E

35E

40E

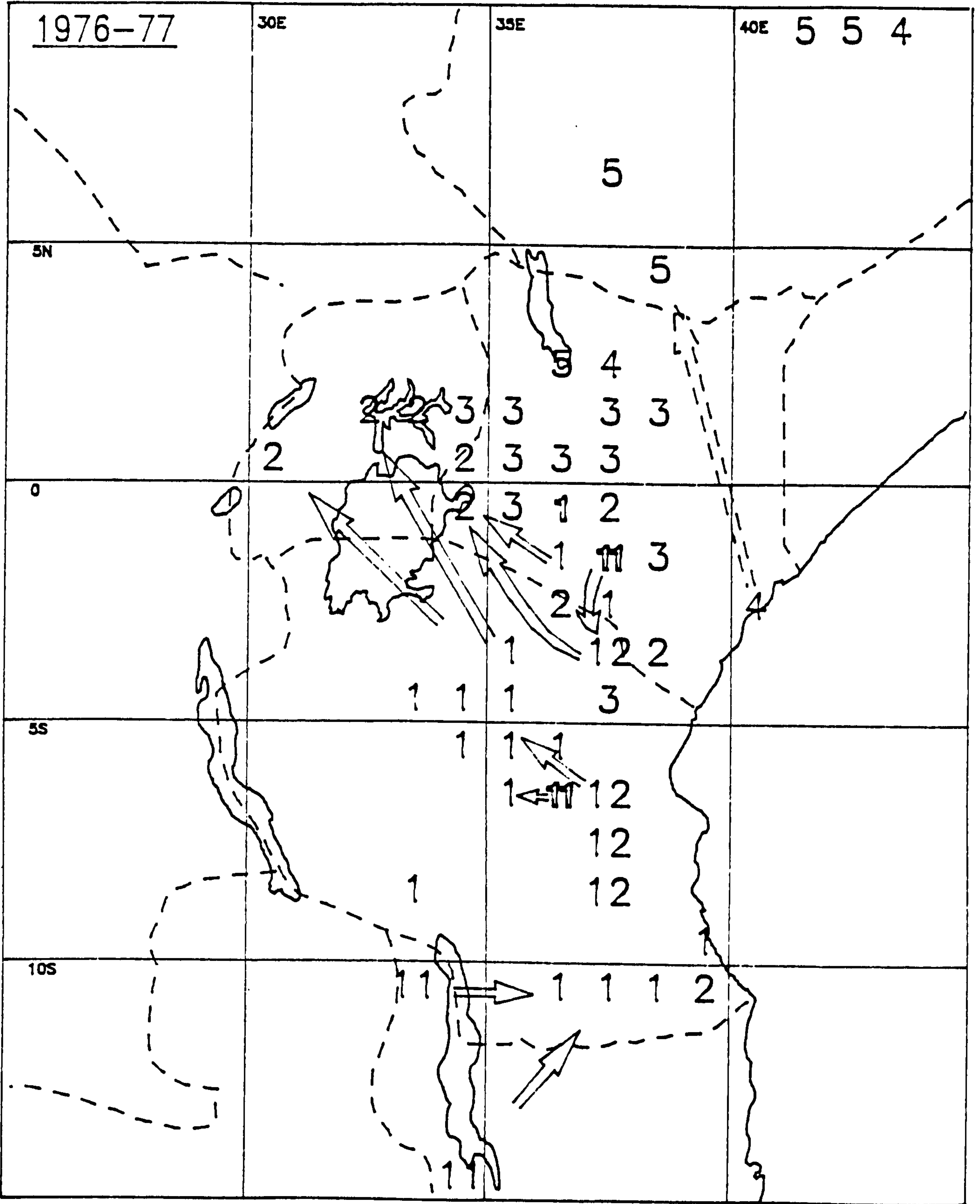
5 5 4

5N

0

5S

10S



There was a late primary outbreak at Nyeri (east-central Kenya) in January, associated with a rainstorm and a large increase in moth catch at Mwea Tebere light trap on 14 January. Moderate trap catches in mid-December indicated that a low density population was present the previous month. Backtracks were from the east or north-east while the only known earlier outbreak was in Kajiado, to the south.

Secondary outbreaks

Some of the moths emerging from the Kajiado primary outbreak at the end of December or beginning of January probably migrated south on northerly winds (Fig.12), giving rise to outbreaks that were reported west of Kilimanjaro in north-east Tanzania. Other moths gave rise to secondaries in Kajiado and Machakos districts (east-central Kenya) but not to the Nyeri outbreak which was too far north. In January, outbreaks were reported over an area of about 16000 ha in the Nachingwea and Tunduru districts of south-east Tanzania. There were no known local sources, but westerly winds from 31 December-3 January (Fig.12), which could have brought moths from Malawi, where there were many large outbreaks in November and December.

The Kilosa primary in November led to about 20 secondary outbreaks (over 8000 ha) in east-central Tanzania in late December, when moth were concentrated by storms at the beginning of the rains. Subsequent downwind migration resulted in outbreaks in Mpwapwa, Singida and Kondoa districts of central Tanzania from mid January to early February. Moths emerging from some of these outbreaks in mid February migrated north-westwards towards Uganda, judging by trajectories, an increase in moth catch at Ukiriguru (south of Lake Victoria) on 17 February, and subsequent outbreaks in Uganda.

Outbreaks in western Kenya (Nyanza and Busia districts) in February may have originated from moths migrating on south easterly winds from north-east Tanzania or Kajiado (east-central Kenya). This migration is supported by the occurrence of an outbreak near Magadi in the Kenya Rift Valley on the probable route.

In February and March, there were large outbreaks in Machakos and Kajiado districts and many small outbreaks in the north towards Mt Kenya (east-central Kenya) originating from earlier outbreaks there. These were associated with rainstorms in late January and February, separated by a dry period.

From March to April, outbreaks appeared further north in Kenya, associated with northward moth migration. In May, outbreaks were reported in southern, central and eastern Ethiopia, and in adjacent north-western Somalia. They may have resulted from moth migration on southerly winds from east-central Kenya, or from an outbreak at Lamu (Kenya coast), although migration to eastern Ethiopia and Somalia would have required at least three nights flight on low-level jet winds of about 15ms^{-1} .

(vi) 1977-78 (Fig.43)

Brief Summary

A very low armyworm season with heavy early rains.

Primary and Secondary Outbreaks

One primary outbreak was reported south Nyanza (western Kenya) in February. There were no secondary outbreaks.

In areas where early season outbreaks usually occur, in Kenya south of the equator and eastern and central Tanzania, rainfall was above average in November and December (Table 15), and rain fell on 16 or more days in November in east-central and western Kenya. These frequent rains probably caused low rates of survival of any caterpillars present and hence led to the lack of outbreaks.

Very few moths were caught in light traps, indicating that overall numbers of armyworm were very low even though the previous season had been severe in both Tanzania and Kenya.

Figure 43. Seasonal summary map for 1977-78 showing the location of primary armyworm outbreaks by month of first occurrence in a degree square. There were no secondary outbreaks.

	OCTOBER		NOVEMBER		DECEMBER	
	1977	1977	1977	1977	1977	1977
	MEAN mm	% OF MEAN RAIN DAYS	MEAN mm	% OF MEAN RAIN DAYS	MEAN mm	% OF MEAN RAIN DAYS
KENYA						
Mombasa	96	309	95	123	70	186
Voi	26	181	106	148	119	175
Makindu	28	11	172	120	115	137
Sultan Hamud	68	6	211	99	98	141
Embu	157	42	259	151	54	87
Nairobi	38	45	134	172	74	101
Kisumu	75	135	120	152	100	84
TANZANIA						
Arusha	25	336	139	68	98	79
Game	30	457	53	132	67	188
DaresSalaam	60	82	122	163	108	172
Morogoro	29	172	61	74	78	215
Kilosa	33	130	96	155	139	198
Dodoma	4	0	20	420	107	134
Mtwara	21	510	53	164	192	66
Nachingwea	7	214	70	0	126	94

Table 15. Monthly rainfall as a percentage of the mean and number of raindays (where available) in Kenya and Tanzania, October-December 1977.

(vii) 1978-79 (Fig.44)

Brief Summary

In Kenya and Tanzania this moderate armyworm season was associated with heavy short rains. Outbreaks in mid December in east-central Kenya may have originated from an outbreak in southern Somalia, but not from the unusual, September to October outbreaks in Ethiopia. Continued heavy rains to February in Tanzania, may explain the lack of secondary outbreaks there. Large-scale westward and north-westward migration from east-central Kenya and north-east Tanzania led to outbreaks in February in western Kenya and the Kenyan Rift valley. The season ended early with no outbreaks in Kenya or Tanzania in April.

Unusual Early outbreaks in Ethiopia

Many outbreaks were reported in central Ethiopia and one in Gamo Gofa (southern Ethiopia) from September to October following the end of the summer rainy season, and during a period when there are usually no outbreaks. They were followed by single outbreaks in late December and early January in Gamo Gofa and Sidamo regions (southern Ethiopia). The previous season had been very low in Kenya and Tanzania and these outbreaks were probably derived from armyworm populations that had persisted in Ethiopia for at least one season. It is not clear whether they were primary or secondary.

Primary outbreaks

In early and mid November, primary outbreaks occurred near Mogadishu (southern Somalia) and at Mbeya (south-west Tanzania) associated with the beginning of the rains. The Somalia outbreak was large (1000 ha) but was

Figure 44. Seasonal summary map for 1978-79 showing primary (bold numerals) and secondary armyworm outbreaks by month of first occurrence in a degree square, and likely migrations between outbreaks from trajectory analyses.

1978-79

30E

35E

40E 4

9 9

9 9 9

9 12 3 1

5N

0

5S

10S

11

2

3

2

3

12

12

12 12 12

12 12

2

12 12 12

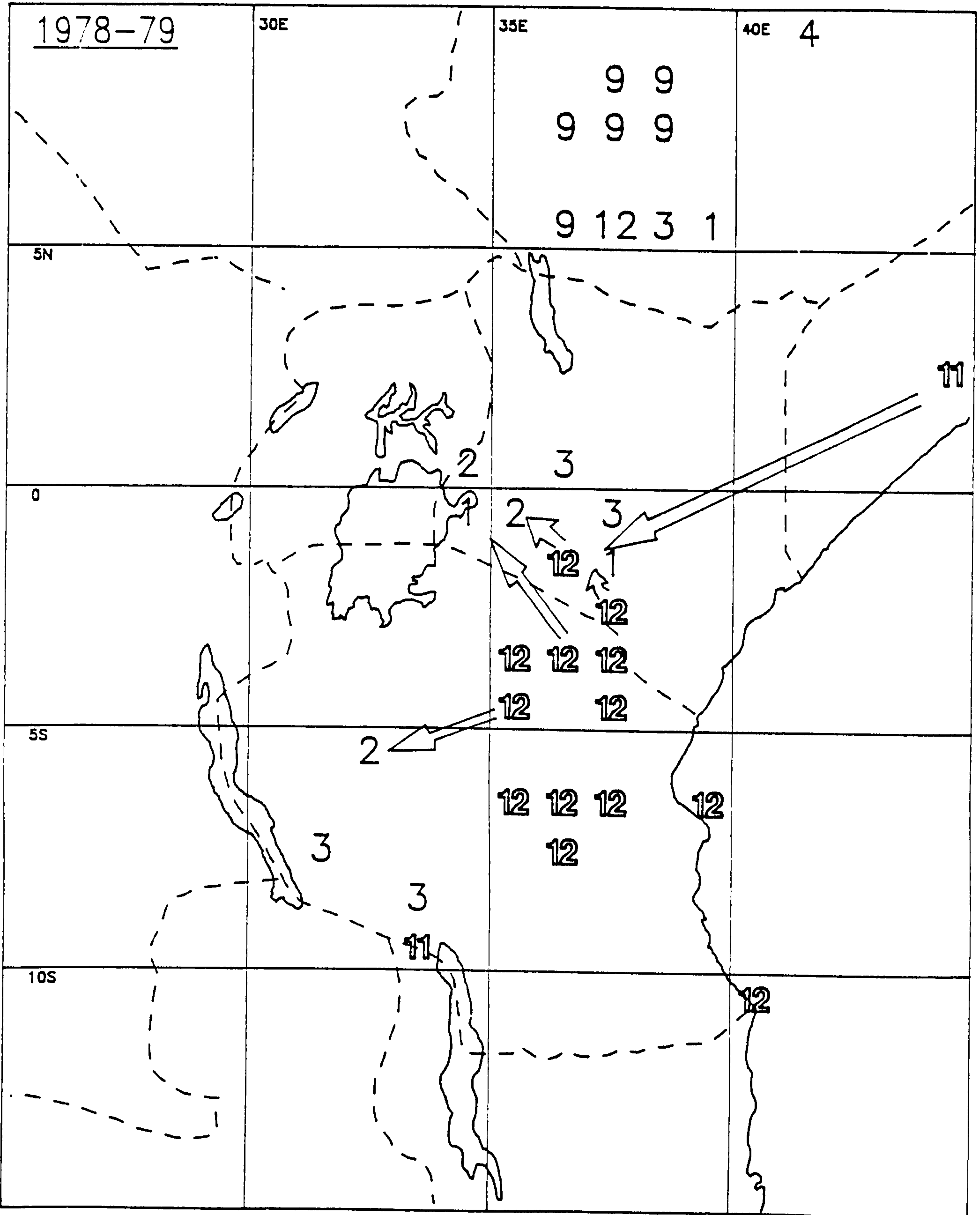
12

3

3

11

12



primary because winds were north-easterly and moths could not have come from known outbreaks in Ethiopia.

Over most of Tanzania, the rains started in mid November, after a dry October, and were then heavy and persistent until mid December with rainfall on an average of 26 days during this period (Table 16). The frequent rainstorms probably prevented outbreak formation in November. Outbreaks occurred widely in east-central, north-east and south-east Tanzania in mid December associated with storms at the end of the rainy period, and with a subsequent mostly dry period in late December and early January.

Outbreaks occurred in Nairobi and Kajiado districts (east-central Kenya) in December, associated with scattered rainstorms at the end of the short rains and small catches of moths in Nairobi NAL pheromone trap from 10 December. No moths were trapped before December, possibly reflecting the lack of armyworm persisting from the previous very low season. Backtracks from the outbreaks indicated that moths came from the north-east (Fig.13). The timing fitted the possibility of moths migrating from the Mogadishu outbreak in about four nights. The December Kenya outbreaks may, therefore, have been secondary rather than primary.

Secondary outbreaks

In Tanzania, very few secondary outbreaks were reported following the December primaries. There was an outbreak at Moshi (north-east Tanzania) in January (associated with a rainstorm on 25 January) and four small outbreaks in central and western Tanzania in February and March. High catches of moths at Tengeru light trap (near Moshi) from 9 January-28 February indicated possible unreported local outbreaks. Outbreaks did occur in late January in

	OCTOBER 1978			NOVEMBER 1978			DECEMBER 1978		
	MONTHLY MEAN mm	% OF MEAN	RAINDAYS	MONTHLY MEAN mm	% OF MEAN	RAINDAYS	MONTHLY MEAN mm	% OF MEAN	RAINDAYS
KENYA									
Mombasa	96	42		95	177		70	220	
Voi	26	62		106	314		119	97	
Makindu	28	625		172	120		115	201	
Nairobi (NAL)	55	195	7	135	99	14	83	159	13
Nakuru	66	153	14	68	88	12	40	165	5
Kisumu	75	139		120	119		100	129	
TANZANIA									
Arusha	25	8	1	139	125	14	98	271	16
Same	30	57	2	53	400	15	67	207	13
DaresSalaam	60			122	348	19	108	148	14
Morogoro	29	17	2	61	285	12	78	328	17
Ilonga	33			79	251	14	144	112	17
Dodoma	4	0	0	20	215	2	107	159	12
Mtwara	21	114	4	53	111	4	192	151	16

Table 16. Monthly rainfall as a percentage of the mean and number of raindays in Kenya and Tanzania, October-December 1978.

neighbouring Taveta (south-east Kenya) which may also have originated from the primary outbreaks in north-east Tanzania in December.

Outbreaks occurred in late January, in Machakos and Kajiado districts (east-central Kenya), and further west at Magadi, in the Rift valley, were derived from the December Kajiado and Nairobi primaries, following large-scale westward moth migration towards the Rift Valley (indicated by high moth catches at Muguga light trap from 24 January-3 February). Backtracks indicated that an outbreak in south Nyanza (western Kenya) in late January also originated from moths migrating from either east-central Kenya or north-east Tanzania. Similar migrations in February (indicated by wind directions and high moth catches) gave rise to a total of 26 reported outbreaks in western Kenya. Many moths also stayed within the Rift valley, giving outbreaks at Mt Margaret and at Nakuru, and in the Nairobi area, where there were five small outbreaks in late February. In March there were two further outbreaks in western Kenya, and two in central Kenya (near Mt Kenya). Winds were mostly easterly although migration from Nairobi outbreaks towards Mt Kenya may have been possible on a few nights. Winds were not suitable for taking moths to Ethiopia in March, and two outbreaks in Sidamo (southern Ethiopia) in late March almost certainly came from armyworm persisting from earlier, local outbreaks. Moths leading to outbreaks in Harar in late April probably came from Sidamo outbreaks, following the seasonal windshift to southwesterly.

(viii) 1979-80 (Fig.45)

Brief Summary

This severe season started late, associated with a late start to the rains in Tanzania and well below average short-rains in Kenya. There were widespread primary outbreaks in eastern Tanzania in December, several of which were large. Primary outbreaks in Kenya were also very large but did not occur until the end of January. In Tanzania, most secondary outbreaks were in Arusha and Kilimanjaro regions, where some were severe. In Kenya, there was a sequence of secondary outbreaks, some very large, persisting until June. Outbreaks in eastern Kenya provided sources for outbreaks in southern Ethiopia in April. Widespread secondary outbreaks not associated with rainstorms (in north-east Tanzania in February and Kitui in March) shows that when parent populations were large, outbreaks could form without moth concentration by rainstorms.

Primary outbreaks

There were two unconfirmed outbreaks east of Kilimanjaro (north-east Tanzania) in November, probably associated with rainstorms recorded in nearby Taveta (south-east Kenya) in early November. October and November rains were below average in both Kenya and Tanzania (Table 17).

The beginning of the rains in Tanzania on 15 December were associated with the first confirmed outbreaks there, which were widespread in Morogoro and Dodoma regions (east-central Tanzania), at Same and Handeni (north-east Tanzania), at Bagamoyo (Tanzania coast) and at two locations in south-east Tanzania. Primary outbreaks at Bagamoyo, Handeni and Kondoa were unusually large (>1000ha each) and caused severe damage to crops. The

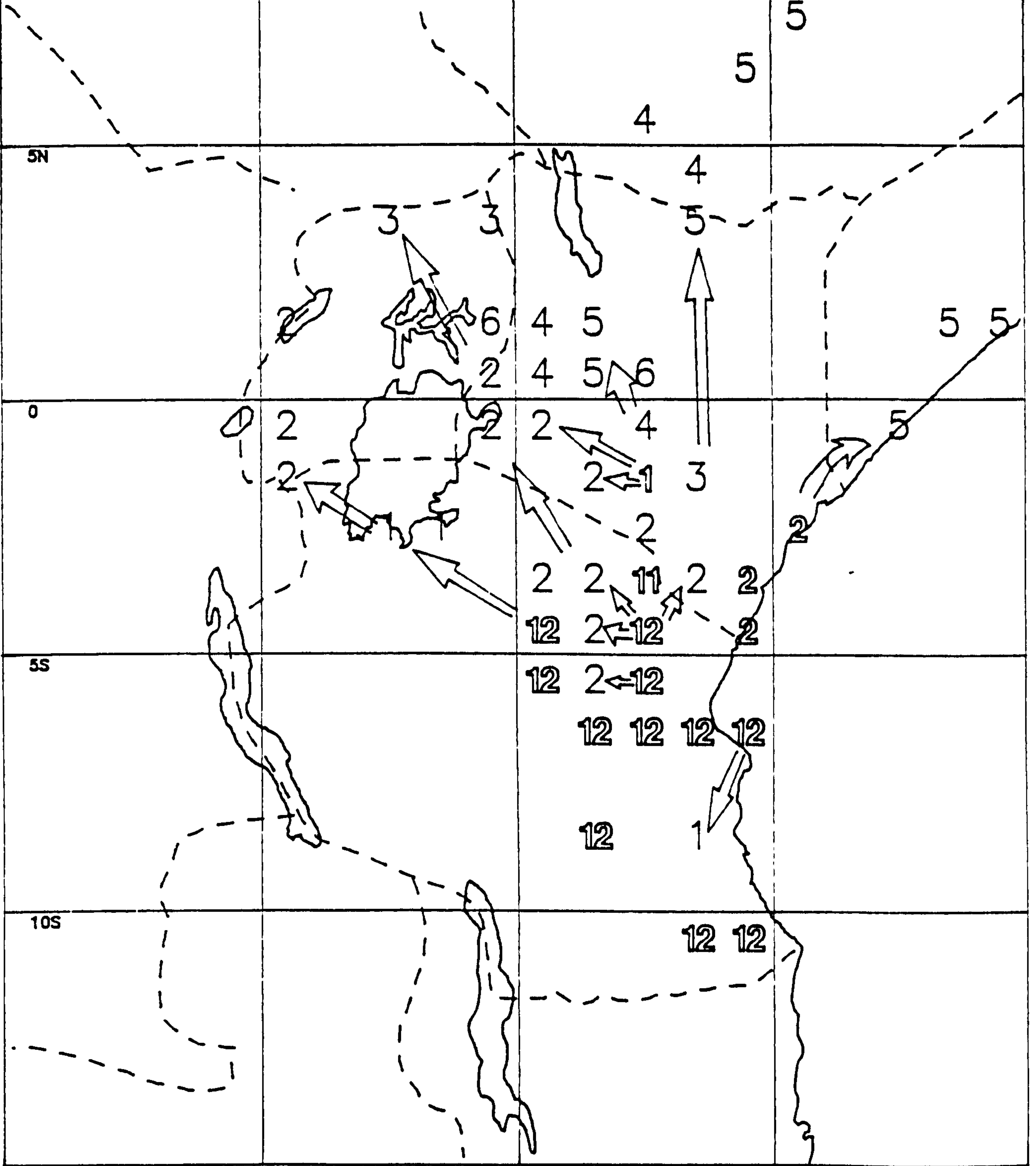
Figure 45. Seasonal summary map for 1979-80 showing primary (bold numerals) and secondary armyworm outbreaks by month of first occurrence in a degree square, and likely migrations between outbreaks from trajectory analyses.

1979-80

30E

35E

40E



large number of primary outbreaks and large size of some of them, suggests that there may have been earlier unreported outbreaks, possibly associated with isolated rainstorms in early November.

Outbreaks were not reported in Kenya until January when were three large outbreaks on pasture in Machakos district (east-central Kenya). They covered a total area of about 6000ha and were associated with rainstorms from 23-28 January, following four dry weeks (Table 18). They were probably primary because moth sources were to the east or north-east, where there were no known earlier outbreaks.

In mid February, there were small primary outbreaks on the Kenya coast, associated with isolated rainstorms following dry weather.

Secondary outbreaks

In January there were secondary outbreaks in Tanzania on the coast, and in Morogoro, Dodoma and Same areas, following nearby primaries; and outbreaks south of Lake Victoria (Mwanza region) following north-westward moth migration.

Then, in February, there were about 50 outbreaks in Arusha and Kilimanjaro regions (north-east Tanzania) probably resulting from moth migration on south-easterly winds from the Handeni primary outbreak. These outbreaks were associated with very high moth catches at Tengeru light trap where about 360000 armyworm moths were caught from 9-22 February, during a period with no rainstorms (Table 18). This indicates that outbreaks can form without rainstorms, when sources are large and there are other concentrating factors, such as mountain winds. Moth catches were also high in March, and moderate in

	OCTOBER					NOVEMBER				
	15	20	25	30	1	5	10	15	20	25
HERU DIST.										
Mikinduru 8937014	X	X	X	X	X	X	X	X	X	X
Meru Met 8937065	X	X	X	X	X	X	X	X	X	X
Giaki Farm 8937072	X	X	X	X	X	X	X	X	X	X
Kianjai 8937021	X	X	X	X	X	X	X	X	X	X
Malthene 8937066	X	X	X	X	X	X	X	X	X	X
ARMYWORM OUTBREAKS										
	Moth arrival									
										Moth emergence
TAVETA DIST.										
Taveta Water 9337110			X		X		X	X	X	X
Kasigau 9338018					X		X	X	X	X
Muangu Rail 9338020							X	X	X	X
Tsavo, Aruba 9338021						X	X	X	X	X
Ngulia lodge 9338027							X	X	X	X
ARMYWORM OUTBREAKS										
	Moth arrival									
										M
TAITA PHEROMONE TRAP										
MACHAKOS DIST.										
Machakos DC 9137010			X		X	X	X	X	X	X
Kiu School 9137012					X	X	X	X	X	X
Pooha 9137014					X	X	X	X	X	X
Katumani 9137089					X	X	X	X	X	X
Rohet 9137115			X		X	X	X	X	X	X
ARMYWORM OUTBREAKS										
	Moth arrival									
										M
MURANGA-EMBU DIST.										
Makuyu Salsal 9037001					X	X	X	X	X	X
Muranga DO 9037007					X	X	X	X	X	X
Murangawater 9037109					X	X	X	X	X	X
Mwea Iebere 9037110					X	X	X	X	X	X
Karaba C.O. 9037177					X	X	X	X	X	X
ARMYWORM OUTBREAKS										
	Moth arrival									
										M
MWEA IEBERE LIGHT TRAP										
KITUI DIST.										
Tseikuru 9038004					X	X	X	X	X	X
Tharaka 9038006					X	X	X	X	X	X
Kitui A.O. 9138000					X	X	X	X	X	X
Kisasi 9138007					X	X	X	X	X	X
ARMYWORM OUTBREAKS										
	Moth arrival									
										M

KEY

Estimated moth arrival leading to outbreaks

Large increase in moth catch

Small isolated moth catch

Rainfall > 9.9mm a day (Rainstorm)

Table 18. Rainstorms and armyworm outbreaks in east-central Kenya. October-November 1980.

April and May but no further outbreaks were reported until May when there were two.

In Kenya, February outbreaks in Taveta and southern Kajiado districts were continuous with those in north-east Tanzania, while small outbreaks in western Kenya and Tororo district (eastern Uganda) probably resulted from moth migration from earlier outbreaks in north-east Tanzania. Isolated outbreaks in western Uganda probably came from moths migrating from Mwanza, Tanzania on south-easterly winds.

In early March there were outbreaks in Kajiado and Machakos (east-central Kenya) associated with widespread rainstorms on 1, 2 March after four dry weeks. Parent moths almost certainly came from the January primary outbreaks in Machakos. Later in March, there were very large outbreaks (estimated total area 50000ha) further east, in Kitui district which probably came from February, Taveta outbreaks. Moth concentration occurred during three dry weeks, possibly associated with topographic winds.

There were further, mostly small, outbreaks in Nyanza (western Kenya) in March and early April. In April, outbreaks also reappeared on the Kenya coast (at Lamu), and appeared further north in Kirinyaga (east-central Kenya), West Pokot (north-east Kenya) and in Gamo Gofa and Sidamo regions (southern Ethiopia). The southern-Ethiopia outbreaks probably originated from moths migrating on southerly winds from outbreaks in Taveta and Kitui districts of Kenya.

In May, outbreaks were widespread in northern and north-western Kenya, and large outbreaks also occurred in southern Somalia, where they probably originated from outbreaks on the Kenya coast following the onset of

southerly winds. The last outbreaks of the season were in Kenya north of the equator, with moth arrival in June.

(ix) 1980-81 (Fig.46)

Brief Summary

This moderate season started early, in October, in east-central Kenya. October primary outbreaks were associated with rainstorms ahead of the short rains. They were followed, in November, by many secondaries in east-central Kenya, and further primaries in south-east Kenya, and north-east, east-central and south-east Tanzania. The season effectively ended in Kenya and Tanzania following secondaries in December, with only isolated outbreaks later in the season. The beginning of the short rains was suitable for rapid population increase in Kenya, but dry weather from mid December to February led to an absence of outbreaks.

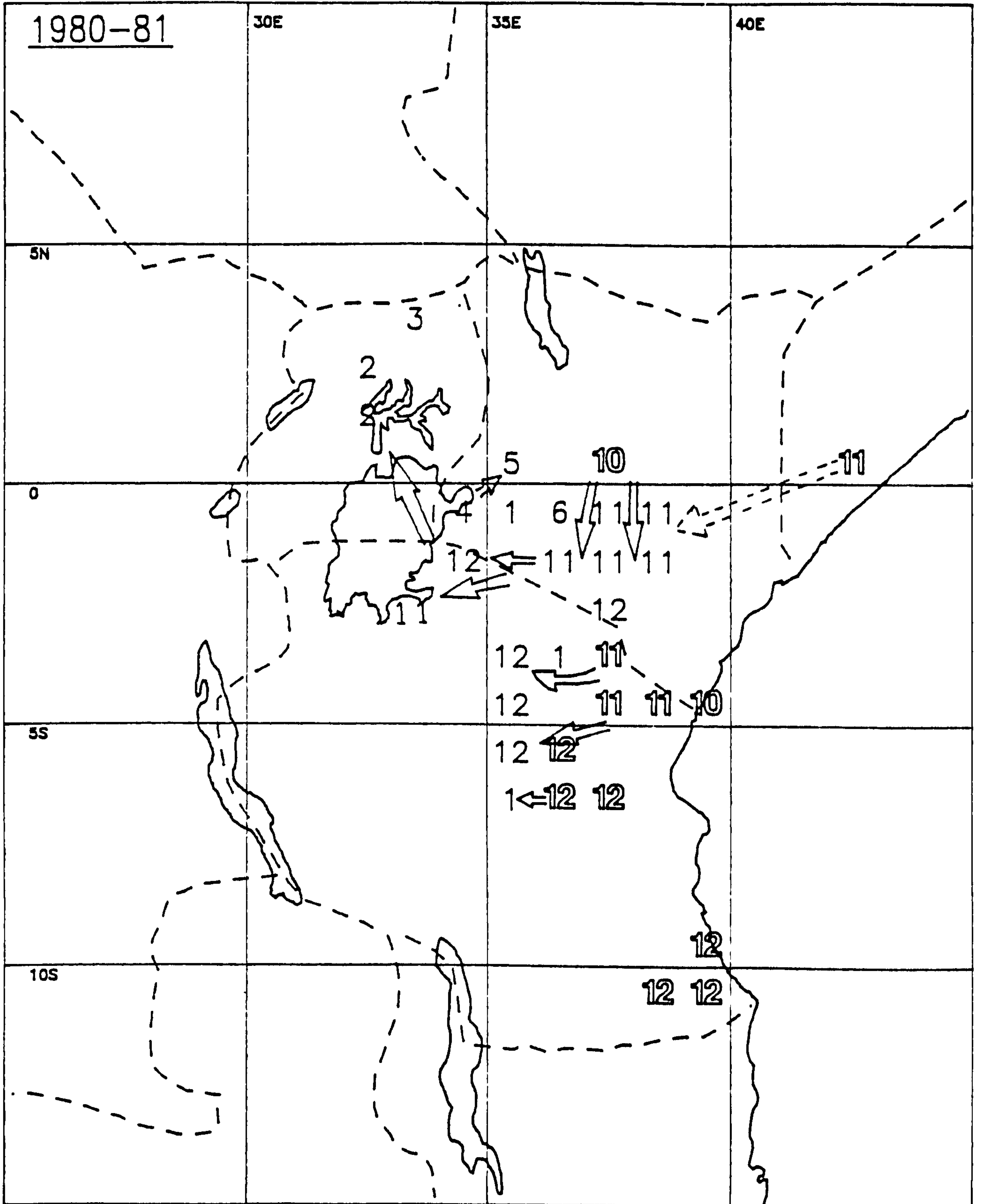
Primary outbreaks

Early primary outbreaks occurred at Kwale (Kenya coast) in early October (details unknown) and in Meru district (east-central Kenya) in mid October. The latter were severe, affecting crops and grass over about 2000 ha, and were associated with rainstorms on 17-19 October, ahead of the wider onset of the short rains on 26 October (Table 19).

In early November, there was a large outbreak (14500 ha), with no known outbreak source, on maize and grass at Jamama (southern Somalia).

In mid November, widespread outbreaks occurred in Taita-Taveta district (south-east Kenya), over about 20000 ha

Figure 46. Seasonal summary map for 1980-81 showing primary (bold numerals) and secondary armyworm outbreaks by month of first occurrence in a degree square, and likely migrations between outbreaks from trajectory analyses.



of maize and grasses, and at Rombo, Same and Lushoto, in adjacent Kilimanjaro and Tanga districts (north-east Tanzania). They were associated with widespread rainstorms from 12 to 17 November after mostly dry weather (Table 14), and were probably too late to have been derived from the Kwale primary, although backtracks came from the Kenya or north Tanzania coast (Fig.10).

An isolated outbreak in Ilonga (east-central Tanzania) in early December was probably also primary. Merrett (1986) shows many more outbreaks, reported in December both in east-central Tanzania and in south-east Tanzania which were not included in my data sources or in Tucker (1993) and, therefore have not been included here.

Secondary outbreaks

In mid-late November, there were widespread outbreaks in Machakos, Kitui, Muranga and Embu districts (east-central Kenya). Estimated moth arrival dates coincided with rainstorms on 17 November, towards the end of the brief short rains. Backtracks for the estimated moth arrival period, 6-20 November (Fig.10) indicated that sources could have been anywhere from the north-north-east to the south-east. However, moth catches at Mwea Tebere (Embu district) indicated a later than calculated moth influx, from 24 November-2 December. This coincided with moth emergence from earlier outbreaks at Meru and in Somalia. Winds were more consistently northeasterly at that time than earlier, and backtracks indicated that both Meru and Somalia were possible sources. An outbreaks at Mwanza (north-central Tanzania) may also have been derived from Meru moths.

In December, there were about 40 small outbreaks in Nairobi, Kiambu and Kajiado districts (east-central Kenya). Backtracks were from the east or south-east.

Most outbreaks were likely to have come from moths migrating from Taita-Taveta primaries but some later outbreaks may have come from November secondaries in east-central Kenya. December was mostly dry but there were isolated rainstorms on 8 and 13 December which may have concentrated moths.

Migration westwards from east-central Kenya led to three outbreaks in Narok district in late December and early January.

Outbreaks in Kondoa and Ngorongoro districts of Tanzania in December were probably derived from the November primaries in north-east Tanzania. Further westward and northwestward migration from northern Tanzania or western Kenya was indicated by the occurrence of heavy outbreaks in central Uganda in February and March.

In February and March, two small outbreaks in Kilimanjaro district were the last of the season in Tanzania. This abrupt end to outbreak occurrence was probably caused by very dry weather in February. There were also no reported outbreaks in Kenya in these months, but armyworm persisted at low density, judging by small trap catches at Kibos (western Kenya), and outbreaks in south Nyanza (western Kenya), and Kitui district (east-central Kenya), in April. The season ended in Kenya with three small outbreaks in Nakuru and Kabarnet districts in May and June. The armyworm situation in Ethiopia was unclear from available data which mentioned caterpillar infestations but suggested that they were probably not armyworms.

(x) 1981-82 (Fig.47)

Brief Summary

This severe season was associated with slightly below average early rains. In late October to November, primary outbreaks in east-central and south-east Tanzania were associated with isolated rainstorms ahead of the main rains. Outbreaks became widespread in eastern and central Tanzania when the rains started in December. Northwestward moth migration led to outbreaks around Lake Victoria in January, and these were severe in western Kenya and southern Uganda. Most of Kenya remained free of outbreaks until the end of March, when moths spread north from northern Tanzania. There were primary outbreaks in southern Ethiopia, and widespread secondaries, possibly with some moths migrating from Kenya coast outbreaks.

Primary outbreaks

In south-east Tanzania there was a small primary outbreak in Nachingwea district in late October, and a large, outbreak, probably primary, on cereals in Tunduru district in mid November. They were both associated with isolated rainstorms ahead of the main rains.

In Morogoro district (east-central Tanzania) a primary outbreak occurred in mid November, near the Uluguru mountains, but there were no rainstorms at Morogoro (the nearest synoptic weather station).

In December, during the rains, primary outbreaks occurred near Same, Korogwe and Handeni (north-east Tanzania) and at Bagamoyo (Tanzania coast).

Figure 47. Seasonal summary map for 1981-82 showing primary (bold numerals) and secondary armyworm outbreaks by month of first occurrence in a degree square, and likely migrations between outbreaks from trajectory analyses.

1981-82

JCE

JEE

5

4CE

5

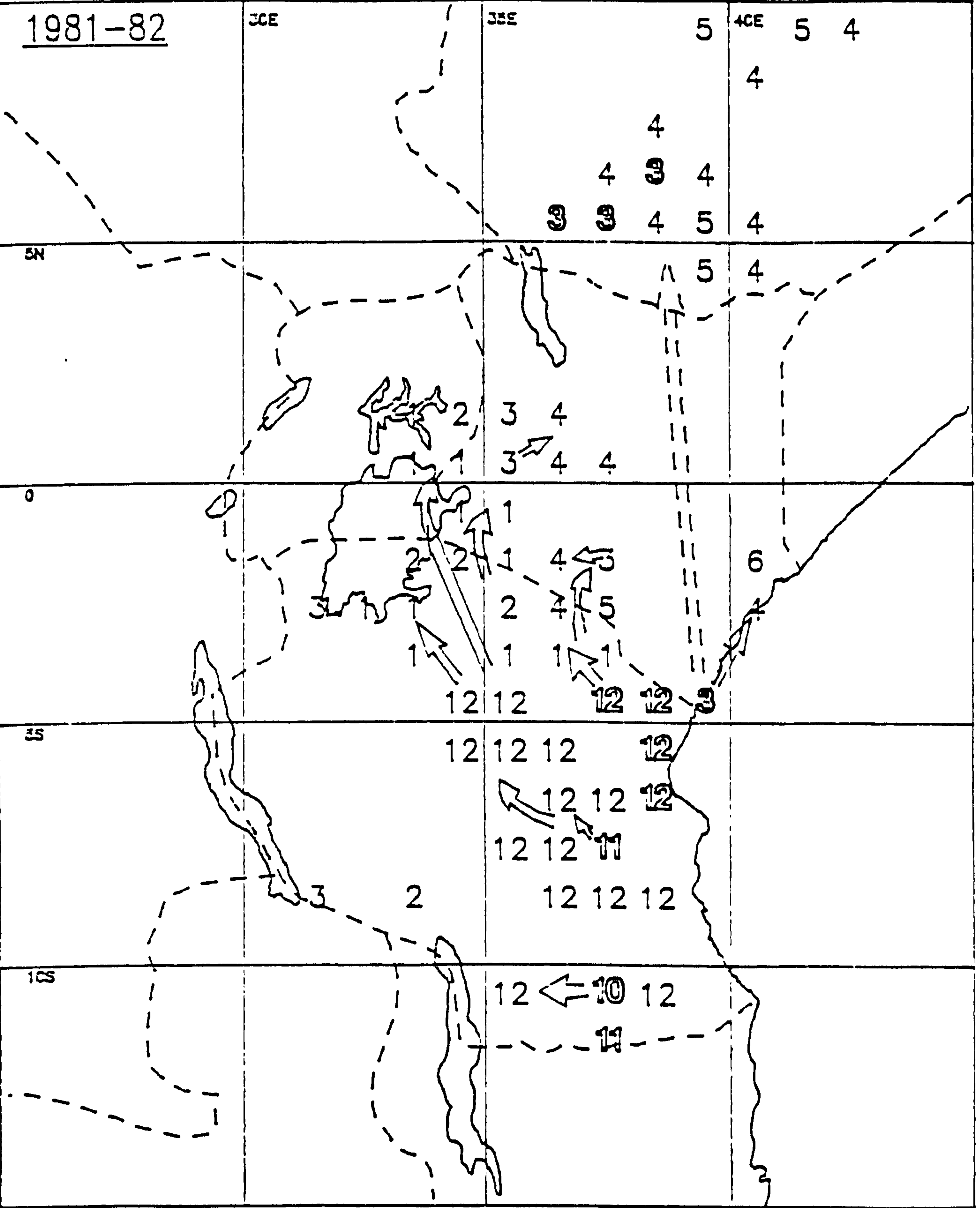
4

5N

0

5S

10S



Three outbreaks in Kwale district (Kenya coast) in late March were probably primaries because winds were onshore easterlies. They were associated with the start of the long rains on 29 March.

Widespread outbreaks in Gamo Gofa and Sidamo provinces of southern Ethiopia in mid to late March were probably primary because, although winds veered to southeasterly on 26 March, there were no known outbreak sources in eastern Kenya or southern Somalia.

Secondary Outbreaks

Over most of Tanzania, the rains started late, at the beginning of December. Then, there were two outbreaks in south-east Tanzania, which may have been derived from the October primary. Outbreaks became widespread in east-central and central Tanzania, downwind of, and at least partly derived from, the November and early December primaries at Morogoro and Same.

Moths emerging from later December primary outbreaks in north-east Tanzania, migrated towards the north-west, judging by forward trajectories (Fig.11). They probably gave rise to January outbreaks in Kilimanjaro and Arusha regions (north-east Tanzania), Taveta district (south-east Kenya) and to at least some of the January outbreaks in western Kenya. Most of north-east Tanzania was very dry in January, and outbreaks occurred only in wetter areas near Kilimanjaro and in the highlands west of Arusha. In western Kenya rainstorms were less frequent than normal but outbreaks were widespread, from Busia to south Nyanza and Masai-Mara, covering an estimated total area of >30000 ha.

In January and early February, outbreaks also occurred in Mwanza and Mara districts (north-central Tanzania),

including Ukerewe Island in Lake Victoria, and in southern Uganda, where some were severe. Winds were south-easterly and backtracks indicated that parent moths came from outbreaks in Singida and Kondoa districts (central Tanzania) and possibly also from north-east Tanzania.

In February a second generation of outbreaks occurred in Uganda and western Kenya, associated with scattered rainstorms, but there were very few outbreaks in Tanzania, probably because of dry weather.

In early and mid March, about 10 outbreaks occurred in north-east Tanzania, associated with an increase in frequency of rainstorms, and about four occurred in western Tanzania. In Machakos district (east-central Kenya) two outbreaks occurred with moth concentration associated with rainstorms from 28-30 March, following dry weather. These rainstorms were associated with a push of southerly winds from northern Tanzania, and moths were likely to have migrated from outbreaks there.

A mark and capture experiment (Rose *et al.* 1985) demonstrated that moths emerging from the Machakos outbreaks migrated westwards, where they almost certainly gave rise to outbreaks that occurred in the Rift Valley (Kajiado and Narok districts) and Nairobi district, from late April to early May.

Further east, moths emerging from primary outbreaks at Kwale (Kenya coast) would have flown northwards (on strong southerly winds). Some probably went along the coast to Lamu and the Tana River, where there were subsequent outbreaks. Others could have flown to southern Ethiopia and contributed to the widespread outbreaks that occurred there in April and May.

Ethiopian outbreaks were also derived from the March primary outbreaks in southern Ethiopia.

(xi) 1982-83 (Fig.48)

Brief Summary

A very low armyworm season, with very heavy early rains preventing armyworm population build-up from small early season primary outbreaks.

Primary outbreaks

In early October a small (2ha) primary outbreak occurred at Voi (south-east Kenya) associated with very early short rains. There were rainstorms near Voi on most days 24-29 September, 6-18 October and from 10 November to 5 December, with more than twice the mean rainfall reported widely in Kenya and Tanzania in October and November (Table 19). No outbreaks were derived from the Voi primary, probably because larvae were killed by heavy rains.

In north-east Tanzania, pheromone traps had small catches of armyworm moths in October, but no outbreaks were reported. In east-central Tanzania there were small (1.5ha), primary outbreaks near Kilosa in late November and near Iringa in early December, associated with rainstorms from 27 November-7 December. There was high larval mortality due to parasitism (Merrett 1986) and heavy rainstorms.

Secondary outbreaks

In January only three very small, low density secondary outbreaks were found in east-central Tanzania, again

Figure 48. Seasonal summary map for 1982-83 showing the location of primary armyworm outbreaks by month of first occurrence in a degree square. There were no secondary outbreaks.

	OCTOBER 1982			NOVEMBER 1982			DECEMBER 1982		
	MONTHLY MEAN	% OF MEAN	RAINDAYS	MONTHLY MEAN	% OF MEAN	RAINDAYS	MONTHLY MEAN	% OF MEAN	RAINDAYS
	mm			mm			mm		
KENYA									
Mombasa	96	208	18	95	91	7	70	80	7
Voi	26	408	13	106	240	11	119	54	9
Makindu	28	529	13	172	231	18	115	137	13
Machakos	52	356	16	193	174	20	122	137	10
Embu	157	289	17	259	51	15	54	70	5
Nairobi	38	387	15	134	111	17	74	153	7
Kisumu	75	225		120	265		100	97	
TANZANIA									
Arusha	25	524		139	224	13	98	101	7
Same	30	460		53	434		67	46	
DaresSalaam	60	302		122	216		108	220	
Morogoro	29	362		61	180	9	78	336	8
Kilosa	33			96	211	11	139	165	12
Dodoma	4	175		20	330	7	107	203	12
Mtwara	21	348		53	228		192	90	

Table 19. Monthly rainfall as a percentage of the mean and number of raindays in Kenya and Tanzania, October-December 1982.

highly parasitized. No further outbreaks were reported during the season, although rainfall from January to April was mostly below average.

(xii) 1983-84 (Fig.49)

Brief Summary

This severe season started late, associated with a late start to the rains (except in south-east Tanzania). Primary outbreaks in mid December in east-central Tanzania were small but led to many secondaries. Primaries in east-central Kenya, in late December to early January, were very large but led to very few secondaries.

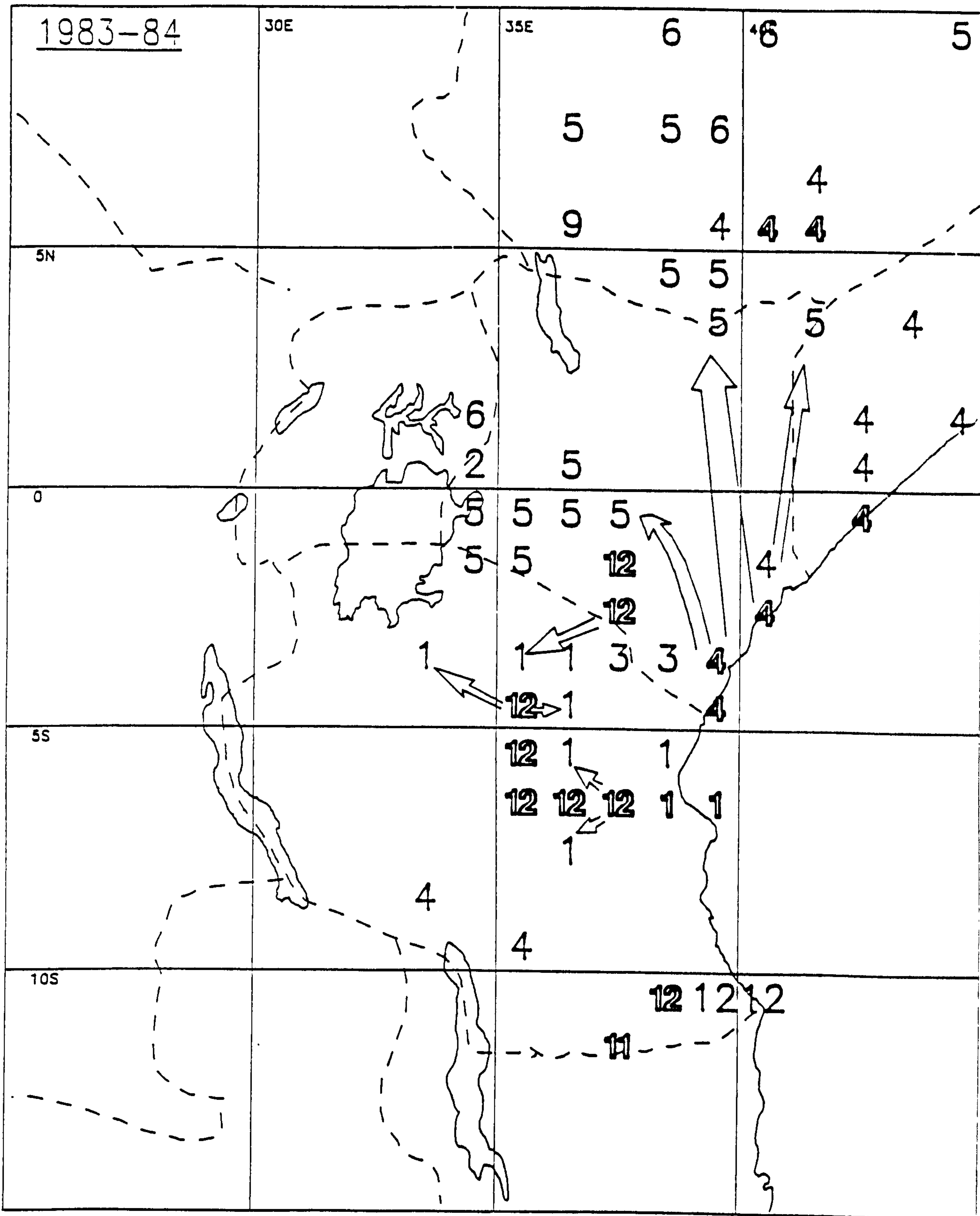
Primary outbreaks on the Kenya coast, in April, were associated with rainstorms following dry weather. Most of Kenya remained dry, as the long rains failed, and late outbreaks were mostly associated with migration from the coastal outbreaks. Late primary outbreaks occurred in southern Ethiopia in April and these were complemented by moths migrating from the Kenya coast in May, leading to severe outbreaks.

Primary Outbreaks

In November, an outbreak occurred at Tunduru (south-east Tanzania) causing severe damage to cereals. It was associated with isolated rainstorms on 20 November. Further east, two outbreaks at Masasi in early December were probably also primary, and were associated with the start of the main rains on 10 December.

In mid December, small primary outbreaks occurred in Mpwapwa, Kilosa, Dodoma and Kondoa districts (east-

Figure 49. Seasonal summary map for 1983-84 showing primary (bold numerals) and secondary armyworm outbreaks by month of first occurrence in a degree square, and likely migrations between outbreaks from trajectory analyses.



central Tanzania) with an estimated total area of 45 ha. They were associated with moth catches from 12-17 December in light and pheromone traps, and with rainstorms, following three dry weeks (Table 20).

In early January, widespread outbreaks occurred near Dar es Salaam (Tanzania coast). These were probably primary as coastal winds were mostly onshore easterlies, except for 9 January when light south-westerly winds were present and migration from east-central Tanzania was just possible.

Very large outbreaks occurred over about 15000ha of pasture in Machakos and Kajiado districts (east-central Kenya), associated with widespread rainstorms from 18-25 December and an isolated rainstorm on 9 January. These were probably primary, as there were no known outbreak sources, either locally or upwind (to the north-east). However, there may have been unreported source outbreaks associated with isolated rainstorms in Machakos district in mid November.

Late primary outbreaks occurred on the Kenya coast near Lamu (early April), Kilifi and Kwale (mid April) and in southern Somalia (mid April). They were associated with isolated rainstorms on 11 April and widespread rainstorms on 19 April, following very dry weather. Winds were southerly, along the coast, so it was unlikely that moths came from the only known possible source outbreaks, in Taita-Taveta district, to the west. Coastal outbreaks covered an estimated area of 20000ha and caused serious damage to maize. Also in April, primary outbreaks occurred in Sidamo region (southern Ethiopia), associated with the beginning of the rains there.

RAINFALL ST.	DECEMBER					JANUARY				
	5	10	15	20	25	30	1	5	10	15
Kinyasungwe 9636020		X		X	X		X	X		X
Mpwapwa 9636000		X		X	X		X		X	X
Ilonga 9637032			X		X			X		X
Wami Prison 9637056				X			X	X	X	X
Mlali 9637051				X	X			X	X	X
MorogoroMet 9637076				X	X			X	X	X

ARMYWORM OUTBREAKS I—Mpwapwa I—Ilonga

ILONGA LIGHTTRAP M H M H M H

KINYASUNGWE PH. TRAP M M

WINDSHIFTS WS→ WS←

MOROGORO WS← No data

DODDHA WS← No data

KEY I— Armyworm outbreak estimated moth arrival
 M Small increase in moth catch
 H Large increase in moth catch
 WS Windshift (Easterlies to westerlies or variable)
 X Rainfall >9.9mm a day (Rainstorm)

Table 20. Armyworm outbreaks, rainstorms and windshifts in east-central Tanzania, December 1983-January 1984.

Secondary Outbreaks

In mid to late December, about 15 outbreaks occurred in Mtwara and Lindi regions (south-east Tanzania). Parent moths could have come from the Tunduru primary outbreak, because there were westerly winds from 22-27 December. Young larvae were reported killed by widespread, heavy rain in late December and early January. No further outbreaks were reported in south-east Tanzania.

In early January, there were about 40 outbreaks in Morogoro region (east-central Tanzania) over an estimated 1100ha of cereals and pasture. Moth concentration was indicated by increases in catch at Ilonga light and pheromone traps on 3 and 7 January respectively, associated with a rainstorm and westerly winds on 3 January. Variable winds meant that moths could have come from December primaries in Morogoro or Dodoma regions, but only if development was rapid (about 23 days). An earlier moth catch at Kinyasungwe on 21 December, associated with rainstorms, indicated the presence of armyworm moths not associated with known outbreaks. Outbreaks at Kondoa and Shinyanga in late January probably came from primary outbreaks in Kondoa district, following slower larval development at higher altitudes. Two outbreaks near Handeni (north-east Tanzania) in late January probably came from moths flying northwestwards from coastal primary outbreaks. Moths emerging from January outbreaks did not give rise to further outbreaks, probably partly due to high larval mortality caused by heavy rains in late January and early February.

Moths emerging from the December-January primary outbreaks in east-central Kenya, would have flown westwards and may have led to two outbreaks in Arusha region (north-east Tanzania) and one small outbreak in Busia district (western Kenya). An absence of other

outbreaks in Kenya was probably caused by very dry weather and a lack of concentrating mechanisms in late January and February.

In March, three outbreaks in Taita-Taveta district (south-east Kenya) and one in Kilimanjaro region (north-east Tanzania) were probably derived from moths emerging from outbreaks in north-east Tanzania at the beginning of March during dry weather. Alternatively they may have been primary with moths concentrated by rainstorms from 11-16 March.

Moths emerging in May from the large primary outbreaks on the Kenya coast, would have flown northwards on strong southerly winds. Backtracks from Moyale (Fig.14) indicate that they could have flown to southern Ethiopia, where there were many, severe outbreaks in May and early June. Northward migration is supported by the occurrence of outbreaks in eastern and northern Kenya. Outbreaks on the Tana River could have originated from the earliest (Lamu) primaries, while outbreaks at Garissa, Wajir, Mandera and Moyale probably come from Kilifi outbreaks. Moths emerging from later outbreaks in Kwale district flew north-westwards, judging by the presence of south-easterly winds, and probably caused outbreaks reported in late May in Nyeri, Kirinyaga and Muranga districts of east-central Kenya. The source of outbreaks at Nakuru and in western Kenya is unknown.

(xiii) 1984-85 (Fig.50)
(largely taken from Pedgley et al 1989)

Brief Summary

This very severe season started early, in east-central Kenya. The short rains were well above average, but dry periods, in mid October and late November, resulted in high armyworm survival. This led to very widespread outbreaks, estimated in November to cover six million hectares in Kenya, making it the most severe season of the sixteen in Kenya. Outbreaks were also widespread in northern Tanzania but not in east-central or south-east Tanzania. The season finished early in most of Tanzania and Kenya. Outbreaks in Ethiopia developed locally and not from migration from Kenya.

Primary outbreaks

Following severe outbreaks in Ethiopia from April to August 1984, an isolated outbreak occurred in Sidamo Province (southern Ethiopia) with estimated moth arrival in late September. This was probably primary because winds were south-easterly and the only possible parent outbreaks, in August, were in central and north-eastern Ethiopia.

Outbreaks then occurred in Meru district (east-central Kenya) associated with the first rainstorms of the short rains, from 2-10 October. An isolated outbreak also occurred in south Nyanza (western Kenya) in early October. There were further outbreaks in Isiolo, Meru, Embu, Kitui and Garissa districts (east-central and eastern Kenya), associated with rainstorms from 20-26 October, and also in southern Somalia. These outbreaks were all primary because winds were south-easterly, so parent moths could not have come from Ethiopia.

Figure 50. Seasonal summary map for 1984-85 showing primary (bold numerals) and secondary armyworm outbreaks by month of first occurrence in a degree square, and likely migrations between outbreaks from trajectory analyses.

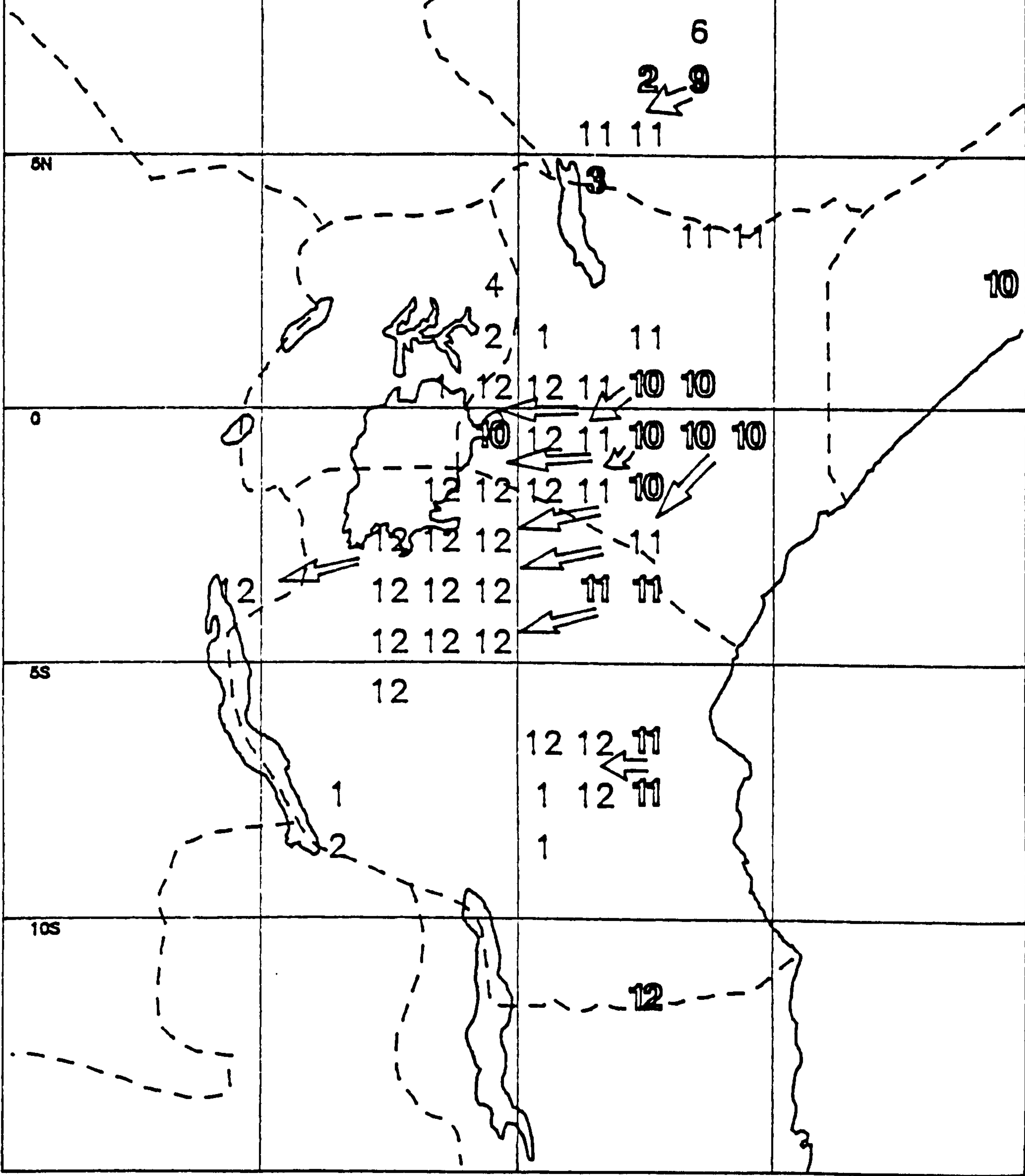
1984-85

30E

35E

40E

3 3→4



In mid November, outbreaks occurred in Arusha and Kilimanjaro districts (north-east Tanzania) associated with the first rainstorms of the short rains there, on 13-17 November. Winds were south-easterly, so parent moths were very unlikely to have come from Kenya primaries. Small numbers of moths caught east of Kilimanjaro in October indicate the presence of a low density, potential source population.

Also in mid November, primary outbreaks in Morogoro region (east-central Tanzania) were associated with the first rainstorms of the season, from 11-18 November. In mid December there were primary outbreaks in Mtwara region (south-east Tanzania), associated with rainstorms from 16-21 December.

In February and March there were late primary outbreaks in Gamo Gofa and Harar provinces of south-west and eastern Ethiopia respectively. Winds were easterly or north-easterly so moths could not have come from Kenya secondary outbreaks (see below).

Secondary outbreaks

Moths emerging in November, from Meru primary outbreaks, migrated at least 200km south-westwards on north-easterly winds. They were concentrated by rainstorms from 3-15 November and led to very widespread, severe outbreaks in east-central Kenya. Moths from late-October primaries in east-central Kenya, flew westwards during a dry spell (from 16-24 November), resulting in outbreaks at low density. Secondary outbreaks also occurred in November in south-western Ethiopia, downwind of the late-September primary.

In December, moths emerging from November secondary outbreaks in Kenya, and primaries in north-eastern

Tanzania, spread rapidly westwards, leading to outbreaks in western Kenya, north-central Tanzania, and even Burundi. There were also further outbreaks in east-central Kenya and north-east Tanzania. Moth arrival for these outbreaks was near the end of the short-rains (10-12 December). In Morogoro region (east-central Tanzania), secondary outbreaks, derived from November primaries, were associated with rainstorms from 4-7 December.

There were a few subsequent outbreaks in Tanzania, mostly in the north-east and in western districts and there were many outbreaks in January in western Kenya, especially in Busia and Kakamega districts, and in neighbouring districts of eastern Uganda. In February, there were large outbreaks on grassland in Machakos and Kajiado districts (east-central Kenya). No outbreaks were reported there with moth arrival in January, probably because there was very little rain, but there must have been a very widespread, low density population derived from December outbreaks.

In March and April there were several secondary outbreaks in western and northern Kenya and one, near Baringo, was reported to be very large. In April there were widespread outbreaks in southern and eastern Ethiopia, derived from the February and March primaries. There was no evidence for migration of moths, leading to outbreaks, from Kenya to Ethiopia.

(xiv) 1985-86 (Fig.51)

Brief Summary

This season started in Kenya where it was severe, with most outbreaks occurring in Kenya and northern Tanzania. The short rains started in Kenya in late October but were below average. Outbreaks were not confirmed until late November when they were widespread. Very few outbreaks were reported in late December to early January but there were widespread outbreaks the following month in northern Tanzania and western Kenya. Some later outbreaks were large, causing considerable damage to crops. There was no evidence for moth migration to Ethiopia where there were primary outbreaks in March.

Primary outbreaks

There was an unconfirmed armyworm outbreak in late October, in Machakos district (east-central Kenya). There were then widespread outbreaks in November. A large (>2000ha) primary outbreak occurred in southern Somalia (south of Mogadishu) in early November. In mid-late November primary outbreaks occurred on the Kenya coast, in Taita-Taveta district (south-east Kenya) and in neighbouring Kilimanjaro region (north-east Tanzania). In late November-early December, outbreaks occurred widely in Machakos, Embu and Muranga districts (east-central Kenya).

November outbreaks were associated with rainstorms during the short rains. In Machakos district the short-rains started on 23 October, five weeks before most outbreaks, but close to the estimated moth arrival date for the unconfirmed outbreak (Table 21). Armyworm populations probably increased in east-central Kenya following the first rains, but may have been supplemented by

Figure 51. Seasonal summary map for 1985-86 showing primary (bold numerals) and secondary armyworm outbreaks by month of first occurrence in a degree square, and likely migrations between outbreaks from trajectory analyses.

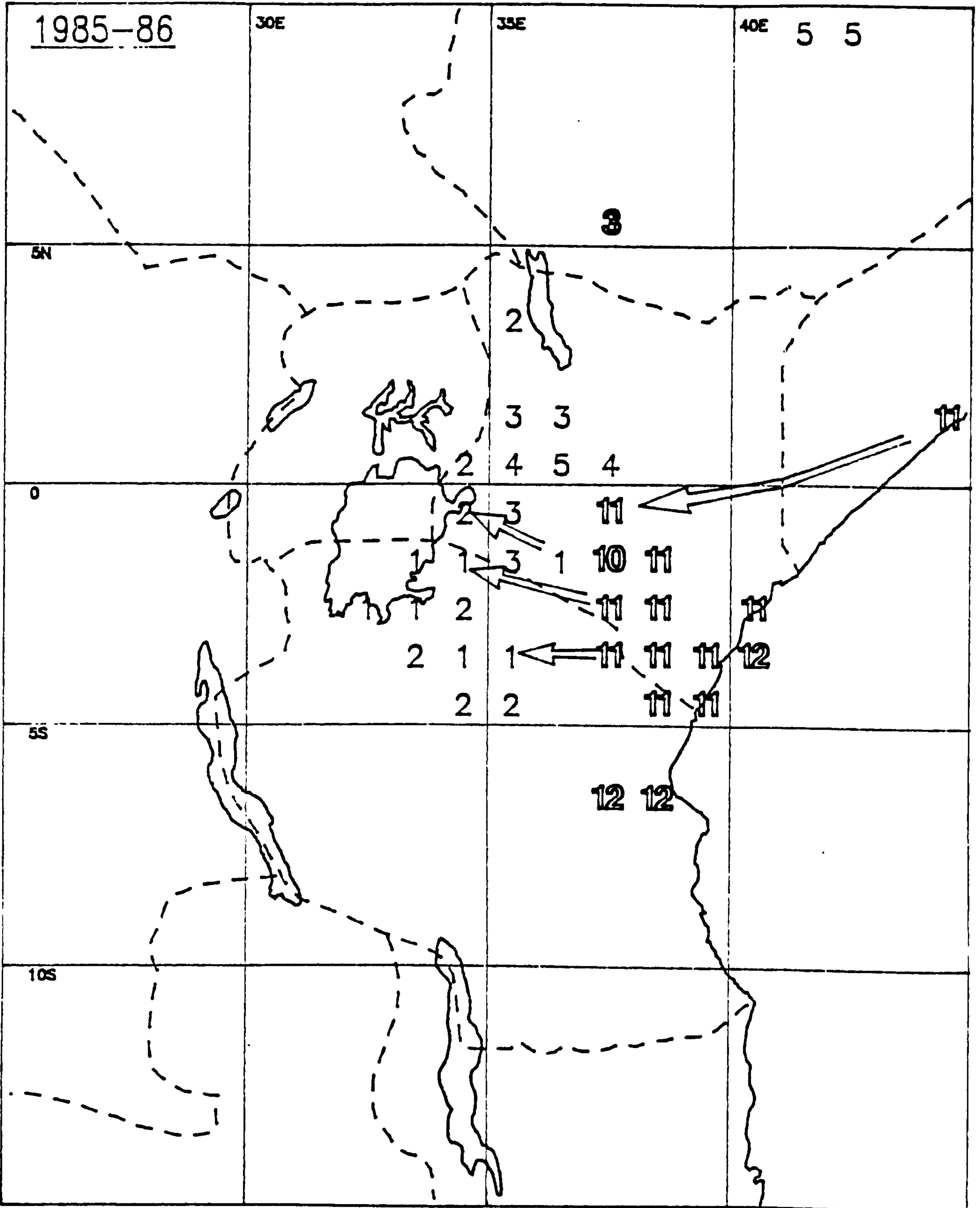
1985-86

30E

35E

40E

5 5



MACHAKOS DIST.	OCTOBER					NOVEMBER				
	20	25	30	1	5	10	15	20	25	30
Kangundo 9137020	X				X	X	X	X		
Sultan Hamud 9137032		X			X	X	X	X	X	
Kithimani 9137074				X		X				
Makueni 9137075		X			X	X		X	X	X
Yatta Sch. 9137117					X					
Hwala 9137119			X	X	X					
Kima 9137124					X	X				
Muthetheni 9137129	X	X			X	X	X	X	X	X
Miu Sch. 9137130	X	X			X	X	X	X	X	X
Kiteta 9137146	X			X	X	X				
Wamungu 9137150				X	X					
Makindu 9237000					X	X				
Simba Rail 9237003					X					
Kiboko 9237018					X	X				
Kabini Hill 9237021					X	X				
Ngulai Plunge 9237028					X	X	X	X	X	X
Mulala 9237035					X	X	X	X	X	X

Start of Rains
 I - unconfirmed - I
 South-easterlies
 South-easterlies
 one generation
 WS NE lies
 WS
 Possible migration ↑
 from Somalia

ARMYWORM OUTBREAKS
 WINDS GARISSA WAJIR
 KEY
 X Estimated moth arrival leading to outbreaks
 WS Rainfall > 9.9mm a day (Rainstorm)
 Windshift

Table 21. Rainstorms and armyworm outbreaks in east-central Kenya, October-November 1985.

immigration. Backtracks from east-central Kenya outbreaks were mostly from the east to south-east in November, giving sources towards the Kenya coast where outbreaks were too late to be sources. On 28 November and 1 December, however, winds shifted towards the north-east (Table 21) and migration from the southern Somalia outbreak may then have contributed to some later outbreaks in east-central Kenya.

In December, primary outbreaks occurred near Dar es Salaam (Tanzania coast) and Morogoro (east-central Tanzania) associated with rainstorms.

In mid March, two primary outbreaks occurred in neighbouring areas of Gamo Gofa and Sidamo provinces (southern Ethiopia), associated with isolated rainstorms. Winds were easterly and there were no known outbreak sources.

Secondary outbreaks

Few secondary outbreaks followed the November-early December primaries. There were two outbreaks, over about 1000ha of grassland, in Machakos district (east-central Kenya), associated with an isolated rainstorm, on 9 January, in an otherwise dry month. Another outbreak occurred near Taveta (south-east Kenya) and there was an unconfirmed report of an outbreak in Kilimanjaro district (north-east Tanzania), where rainstorms were more frequent. Moths emerging from these outbreaks would have flown westwards towards Lake Victoria.

From the end of January to early February there were widespread outbreaks in Nyanza and Busia districts (western Kenya), and in north-central Tanzania, from western Arusha region to Lake Victoria. At Hanang

(Arusha region) a serious outbreak of about 500 ha occurred on commercial wheat and barley.

From late February to early March there were further secondary outbreaks in western Kenya, with a large outbreak on wheat and grassland in western Narok district and an outbreak in Machakos district (east-central Kenya). In northern Tanzania, there were outbreaks in Serengeti, associated with high trap catches from 8-10 March and scattered rainstorms, and a very large (2000 ha) outbreak on the Hanang wheat scheme (Arusha region). Rainstorms from 5-7 March and 16-17 March probably concentrated moths emerging from the earlier outbreak and prevented their dispersal away from the area.

In late March and early April there were scattered outbreaks in east-central, central, western and north-western Kenya, derived either locally or from moths migrating from northern Tanzania. There were no further outbreaks in Tanzania. Three outbreaks occurred in Hararghe Province (eastern Ethiopia) in early May, possibly derived from primaries in southern Ethiopia in March.

(xv) 1986-87 (Fig.52)

Brief Summary

The season was severe in Tanzania, although early rains were heavy, especially in December. In Kenya outbreaks were mostly in the west and the season was only moderate. A sequence of outbreaks occurred from Morogoro region north-westwards towards Lake Victoria, and another from north-east Tanzania to western Kenya and eastern Uganda. In south-west Ethiopia, armyworm survived the dry season, giving rise to primary outbreaks in February and March, and later secondaries.

Primary outbreaks

In early October, primary outbreaks occurred in Busia district (western Kenya), associated with isolated rainstorms, and in Gamo Gofa province (southern Ethiopia). The sources were probably local, with low density armyworm persisting from the previous season.

In late October, two small primary outbreaks occurred near Morogoro (east-central Tanzania) associated with a small catch of moths on 28 October, but no nearby rainstorms (Table 22). In November about 25 outbreaks occurred in Morogoro region, associated with large increases in moth catch at Morogoro and Ilonga pheromone traps from 14-27 November, and rainstorms from 13-26 November. Most of these outbreaks were primary, but a few later ones may have been derived from the October primaries. Winds were easterly, so sources were local or towards the coast where rainstorms in mid October may have resulted in a large increase in low-density populations.

Figure 52. Seasonal summary map for 1986-87 showing primary (bold numerals) and secondary armyworm outbreaks by month of first occurrence in a degree square, and likely migrations between outbreaks from trajectory analyses.

1986-87

30E

35E

40E

5N

0

5S

10S

5

4 10

3

4

4

4

2

7

12 12 12

12 12 12 11 10

12

11

12 11 10 12

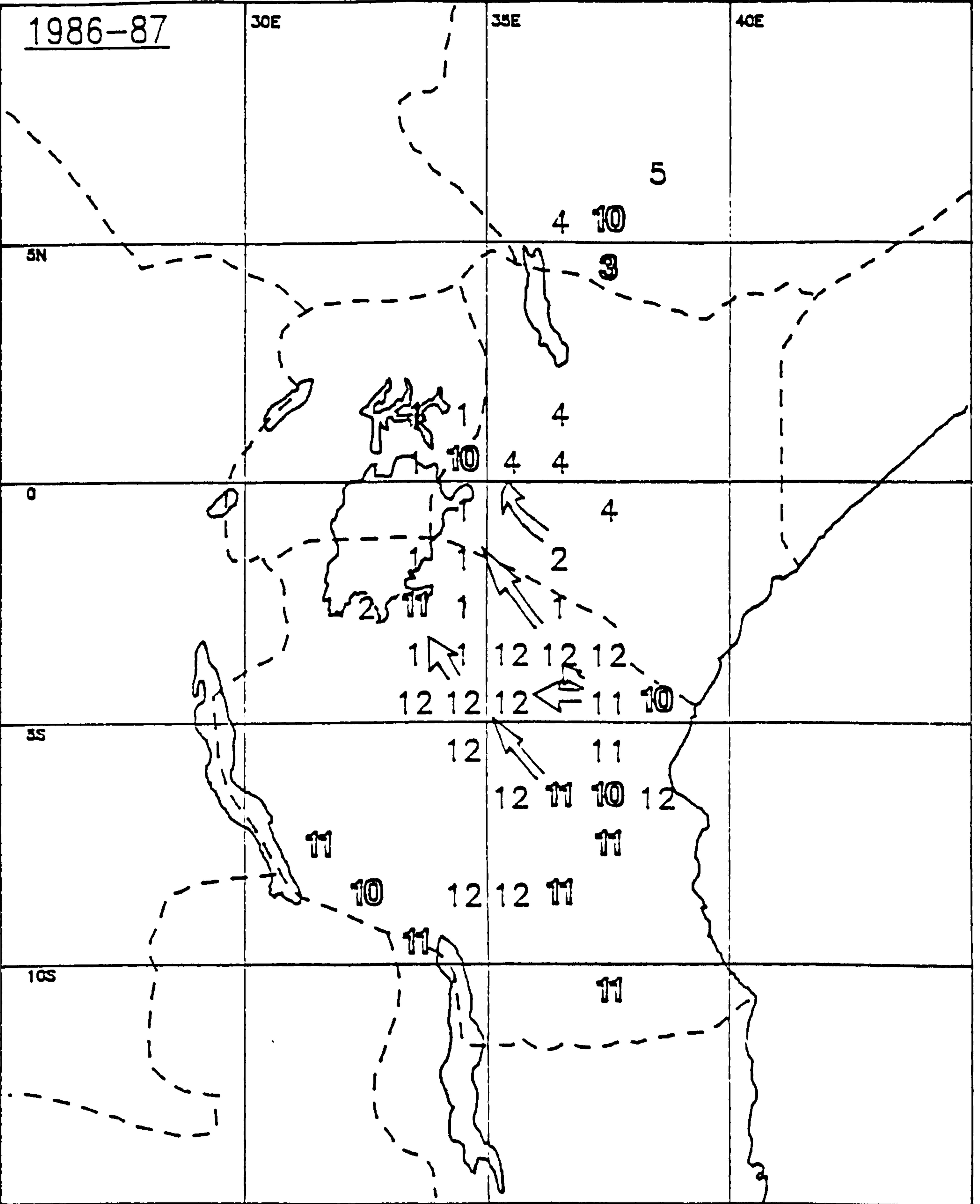
11

11

10 12 12 11

11

11



	OCTOBER					NOVEMBER					30
	25	30	1	5	10	15	20	25	30	1	
RAINSTORMS											
Morogoro Met 9637076					X	X	X	X	X	X	
Morogoro Agr 9637000					X	X	X	X	X	X	
Ilonga 9637032					X	X	X	X	X	X	
Mkata Ranch 9637089						X	X	X	X	X	
Mpwapwa 9636000		X	X	X	X	X	X	X	X	X	X
ARMYWORM OUTBREAKS											
MOTH CATCHES											
Morogoro light trap					m	m	m	m	m	m	M
Morogoro pher. trap											M
Ilonga pher. trap											M

KEY

- Estimated moth arrival leading to outbreaks
- Large increase in moth catch
- Small increase in moth catch
- Rainfall >9.9mm a day (Rainstorm)

Table 22. Rainstorms and armyworm outbreaks in east-central Tanzania, October-December 1986.

Elsewhere in Tanzania, there were two primary outbreaks in Lushoto district (north-east Tanzania) associated with rainstorms from 26 October-1 November, a primary outbreak at Mwanza (north-central Tanzania) in late November, and two small primary outbreaks in Tunduru (in the south-east) associated with the start of the rains in mid November. In south-west Tanzania, two outbreaks occurred near Mbeya in late October and mid November, and there were two more (one of 3200ha) in Sumbawanga district. These outbreaks were also primary unless there were outbreak sources in Malawi (for which no data were available).

In February there was a primary outbreak in Gamo Gofa province (southern Ethiopia) associated with isolated rainstorms. Small trap catches of moths indicated that armyworm at low density, persisted there from the October outbreak. Three weeks later, there were widespread outbreaks in Gamo Gofa and western Sidamo provinces, associated with rainstorms in mid March, but probably too early to have been derived from the February outbreak.

Secondary outbreaks

In late November, there were two outbreaks at Handeni and one at Same (north-east Tanzania) which probably came from moths flying westwards from primaries near Lushoto. In December to early January north-westward migration led to further outbreaks near Arusha and Moshi (north-east Tanzania) and in adjacent areas of Taveta and Kajiado districts (south-east and east-central Kenya).

During December, there were also very widespread outbreaks in central Tanzania, in Dodoma and Singida regions and in Hanang district of southern Arusha region. They covered a total area >80000ha, and parent moths came from Morogoro primaries, judging by backtracks (Fig.53).

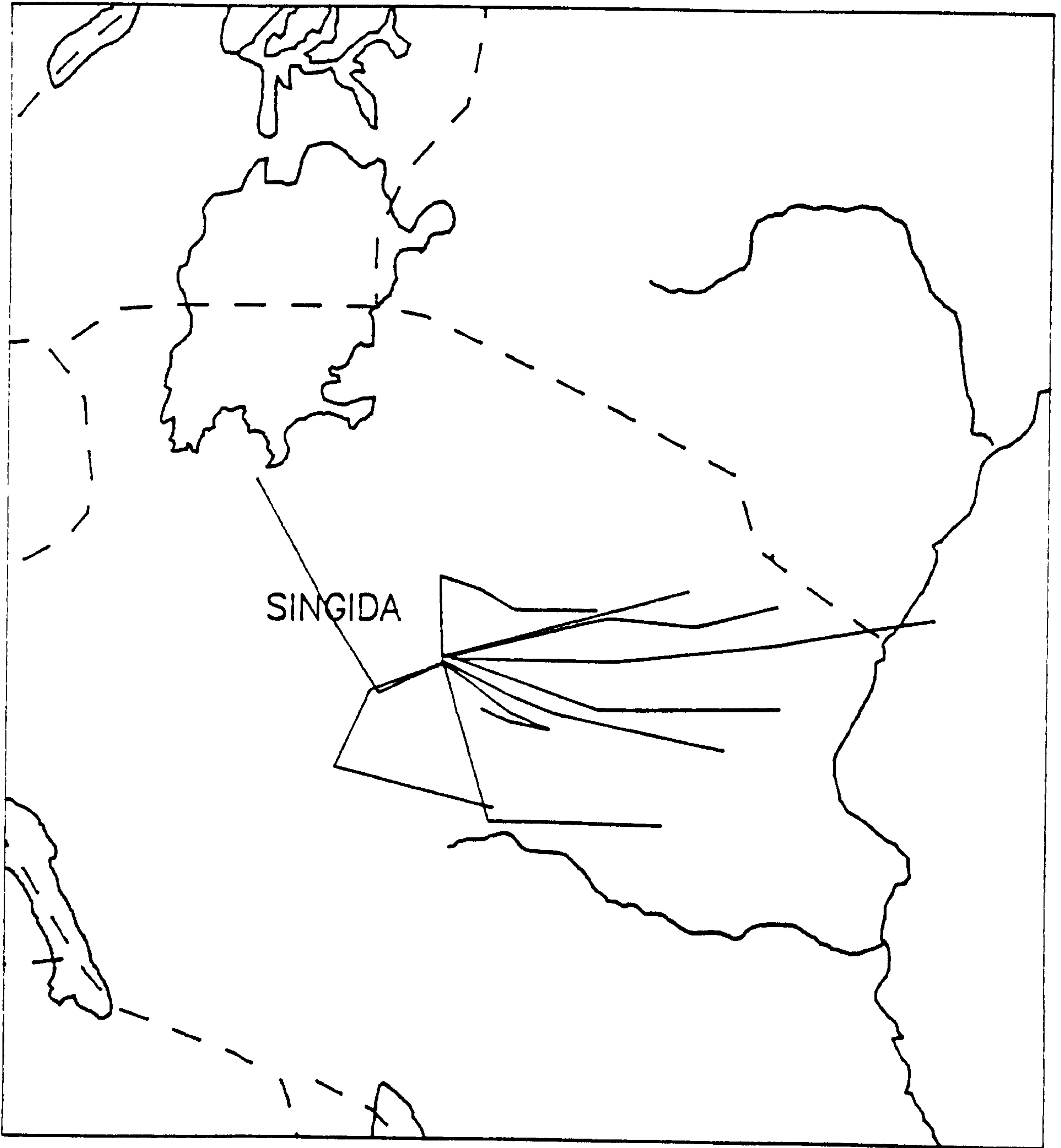


Figure 53. Backtracks from outbreaks in Singida region with moth arrival 1-31 December 1986.

This indicates that control measures in Morogoro region had failed to prevent large-scale moth migration. These secondary outbreaks were associated with widespread rainstorms during December, and a well above average rainfall total. Control measures were again carried out, and heavy rain, which continued into January, was reported to have killed armyworm in Dodoma Region.

Three small outbreaks in Mwanza region (north-central Tanzania), in late December, were probably derived from the outbreak there the previous month.

In mid-late January about 50 outbreaks occurred on cereals in Shinyanga, Mwanza and Mara regions (north-central Tanzania) associated with below average rainfall. Most outbreaks were small and the estimated total area was about 800ha. Backtracks were mostly from the south-east, with parent moths for Shinyanga outbreaks coming from Singida and parent moths for Mara outbreaks coming from Arusha outbreaks. Outbreaks also occurred in January in Nyanza region and Masai-Mara (western Kenya), and Tororo and Mbale districts (eastern Uganda), with backtracks indicating sources in north-east Tanzania. Outbreaks in Kenya were larger than those in Tanzania, covering an estimated total area of 1000ha of agricultural land and 2000ha of wild grassland.

Further outbreaks in Tanzania occurred only in the north-east, in Arusha and Kilimanjaro regions, in March and April. In Kenya, there were further outbreaks in February in Nyanza region and two small outbreaks in Kiambu district (east-central Kenya). Kiambu outbreaks probably came from moths flying north-westwards from Kajiado, being concentrated by isolated rainstorms on 18-19 February. Further outbreaks occurred in Kajiado district (east-central Kenya) in March and April, and in April there were also outbreaks further north in Embu

(east-central Kenya), Baringo and Uasin Gishu districts (north-west Kenya). Outbreaks in Gamo Gofa and Sidamo regions (southern Ethiopia) in April and May almost certainly came from earlier outbreaks there. An absence of late Ethiopian outbreaks may have been partly due to a lack of moth migration from Kenya.

(xvi) 1987-88 (Fig.54)

Brief Summary

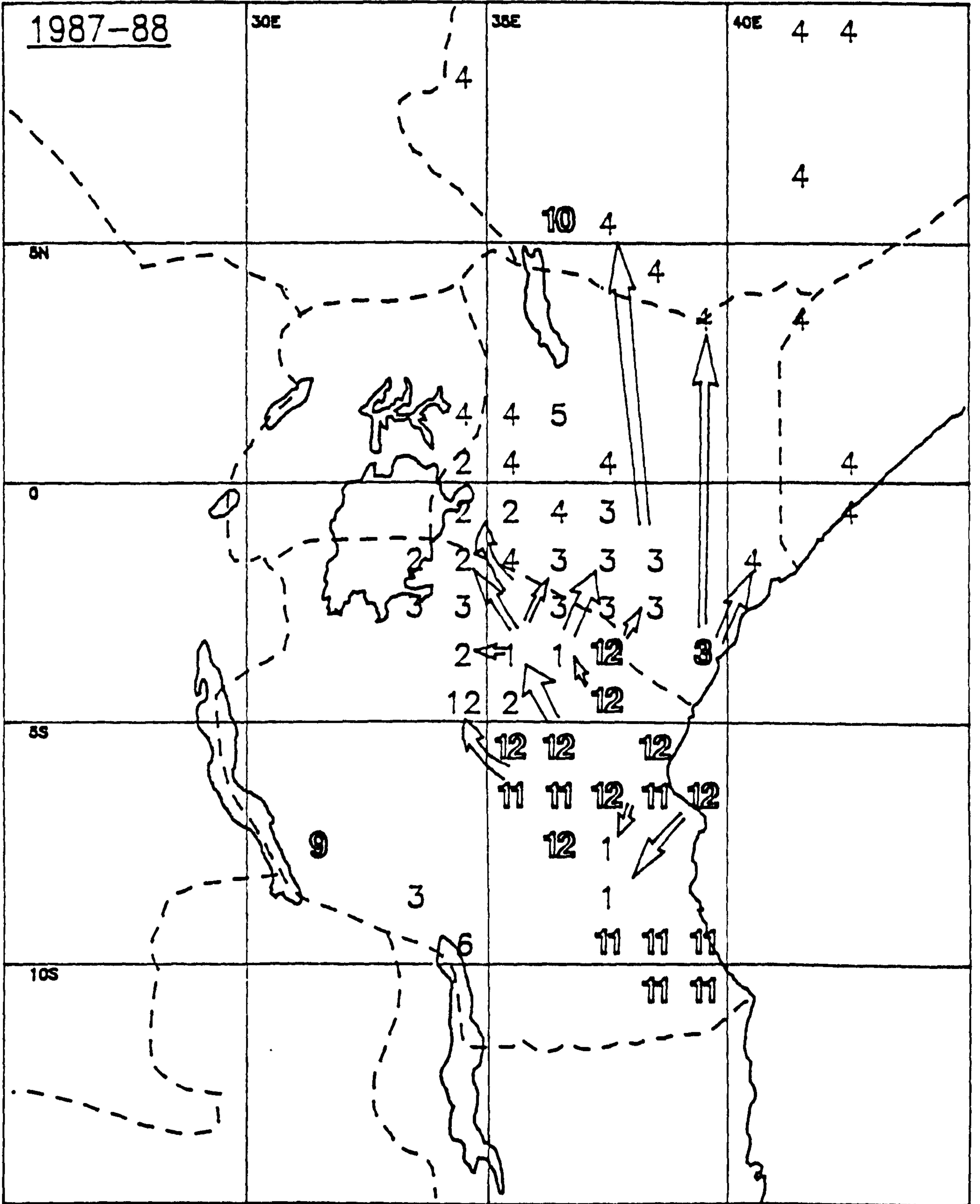
In this severe armyworm season the October-December rains were well below average in both Kenya and Tanzania. Widespread primary outbreaks occurred in south eastern Tanzania, in early November before the onset of the rains, and in east-central Tanzania in late November, with the start of the rains. Subsequent outbreaks were in northern Tanzania, following northwestwards migration from east-central Tanzania. An incursion of south-westerly winds in mid March led to early moth migration into east-central Kenya. In April, after winds became south easterly, there was further northward migration, towards northern Kenya and southern Ethiopia.

Primary outbreaks

In early October, a small primary outbreak occurred in Gamo Gofa (southern Ethiopia) associated with isolated rainstorms.

There was a very early, unconfirmed report of an outbreak in Rukwa region (south-western Tanzania) in September. In early November, primary outbreaks were widespread in Mtwara and Lindi Regions (south-east Tanzania), associated with dry weather and isolated light falls of rain. Widespread rainstorms occurred in late November

Figure 54. Seasonal summary map for 1987-88 showing primary (bold numerals) and secondary armyworm outbreaks by month of first occurrence in a degree square, and likely migrations between outbreaks from trajectory analyses.



when outbreaks were already present. In early November an outbreak also occurred near Dodoma (east-central Tanzania), with moth concentration associated with isolated rain (8.6mm) in a mainly dry period.

From late November to early December over 40 outbreaks occurred in Dodoma and Morogoro regions (east-central Tanzania), with an estimated total area of about 3300ha. Two early outbreaks were associated with rainstorms on 25 November and a small catch of moths at Ilonga (Table 23). Most outbreaks were associated with more persistent rainstorms, and large increases in moth catch, from 9-11 December. There were also two small primary outbreaks near Dar es Salaam (Tanzania coast), associated with rainstorms on 29 November and 10 December, and one at Same (north-east Tanzania) in early December.

From late December to early January widespread outbreaks occurred in Taveta district (south-east Kenya) and Kilimanjaro region (north-east Tanzania), associated with isolated rainstorms in a mostly dry period. These outbreaks were mostly primary, but some in Kilimanjaro region may have come from moths migrating northwestwards from the Same primary.

An outbreak at Kilifi (Kenya coast) in March, associated with isolated rainstorms at the start of the long rains, was probably a late primary outbreak.

Secondary outbreaks

In mid December, there were secondary outbreaks in Lindi region (south-east Tanzania), derived from November primaries. There were also three outbreaks in Singida region (central Tanzania), associated with an increase in moth catch and rainstorms from 9-15 December, after a dry

	10	15	20	25	30	5	10	15
Hombolo								
Dodoma				X				
Mwapwa				X			X	
Ilonga			No data					
MorogoroMet		X		X			X	
Kilombero	X			X				
Ruembe	X			X				

	10	15	20	25	30	5	10	15
TRAP CATCHES								
Ilonga Ph. trap								
Ilonga light trap								
ARMYWORM OUTBREAKS								

	5	10	15	20	25	30	1	5	10
Mutomo			X		X			X	
Muthue			X	X	X			X	
Kisasi				X	X			X	X
Itumba			X	X	X			X	X
Ikutha			X	X	X			X	X
Matinga			X	X	X			X	X

	5	10	15	20	25	30	1	5	10
EAST-CENTRAL KENYA (KITUI)									
ARMYWORM OUTBREAKS									

KEY

————— Estimated moth arrival leading to outbreaks
 m Small increase in moth catch
 M Large increase in moth catch
 X Rainfall >9.9mm (Rainstorm)

Table 23. Rainstorms and armyworm outbreaks in east-central Tanzania, October-December 1987.

period. Backtracks indicated moth migration from the early Dodoma outbreak.

In January, small outbreaks occurred in Mbulu district, south-west of Arusha (north-east Tanzania). Winds were south-easterly and backtracks indicated that parent moths probably came from primary outbreaks in east-central Tanzania. Secondary outbreaks also occurred in Morogoro region (east-central Tanzania), associated with rainstorms in mid January following mostly dry weather.

In February, outbreaks, derived from local secondaries, occurred in Singida region and Mbulu district, and there were also outbreaks in Arusha and Kilimanjaro regions (north-east Tanzania), probably coming from the January primary outbreaks there. Outbreaks also appeared in Mara region, east of Lake Victoria (north-central Tanzania), western Kenya and Tororo district (eastern Uganda). Back-tracks indicated that parent moths came from north-east Tanzania.

In March, there were further, widespread outbreaks in Mara and Kilimanjaro regions of Tanzania, and a few outbreaks in western Kenya. The last outbreaks in northern Tanzania were in early April, mostly in Arusha and Kilimanjaro districts. However in south-west Tanzania, very unusual outbreaks were reported from near Njombe (Iringa region) in June.

In mid-late March, there was a large-scale moth migration from north-east Tanzania to east-central Kenya, leading to about 50 outbreaks in Machakos, Kitui and Kajiado districts covering an estimated 3000ha. A network of pheromone traps in Machakos and Kitui districts showed widespread increases in moth catch from 19-21 March, associated with rainstorms from 18-26 March and an incursion of south-westerly winds across much of Tanzania

and into southern Kenya from 18 to 22 March. Backtracks (Fig.55) showed possible migration routes from northern Tanzania or from eastern Kenya with an area of wind convergence in the Kitui/Mackakos area.

From 26 March, winds veered to south-easterly or southerly over central and eastern Kenya. The appearance of armyworm outbreaks near Mt. Kenya (east-central Kenya), Marsabit (northern Kenya) and in Sidamo region (southern Ethiopia) indicated widespread northward moth migration from north-east Tanzania and east-central Kenya at the beginning of April. Further east, outbreaks at Moyale, Mandera and Wajir (northern Kenya), Tana River (eastern Kenya) and southern Somalia probably came from moths migrating from the primary outbreak at Kilifi (Kenya coast). In western Kenya, widespread outbreaks in Trans Nzoia district in early April also indicated northward moth migration from March outbreaks.

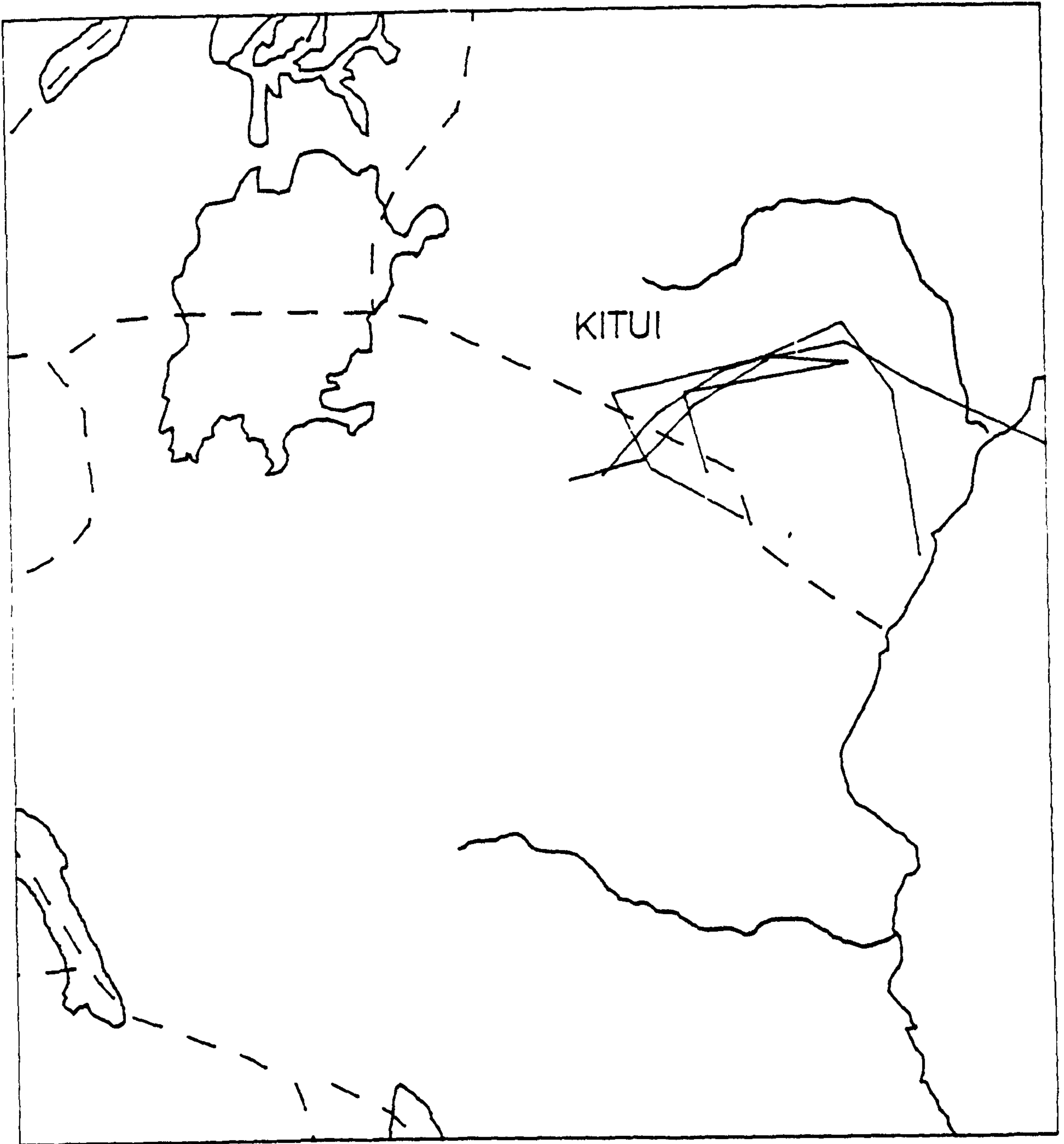


Figure 55. Backtracks from outbreaks in Kitui district with moth arrival 18-24 March 1988.